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Cover photo: *Myrmarchne formicaria*, an exotic salticid recently discovered in northeastern Ohio. Photo by Rich Bradley.

PESTICIDES AFFECT THE MATING BEHAVIOR OF
RABIDOSA RABIDA (ARANEAE, LYCOSIDAE)

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ABSTRACT. The effects of exposure to a single sublethal dose of the pesticide malathion on the courtship and mating behavior of the lycosid, *Rabidosa rabida* (Walckenaer 1837) is explored. Animals were tested in combinations where one or both sexes were exposed to the insecticide. The data indicate that while there was no effect on the patterning of courtship behavior, control males initiated courtship more rapidly than dosed animals. Mating behavior was severely disrupted and resulted in most dosed males being killed by females without achieving copulation.

Keywords: Malathion, courtship, reproductive behavior, insecticide

Many insecticides kill both target and non-target species by affecting specific sites within the nervous system. Since an animal's behavior is governed by interactions among nerve cells, it is not surprising that even low doses of pesticides can influence behavior. While most research on sublethal doses of pesticides has concentrated on economically-important insects (Haynes 1988), few studies have assayed the effects on this aspect of spider biology. This is surprising given that spiders are known to reduce and help regulate insect pests (Luczak 1979; Mansour et al. 1980; Winfield et al. 1992; Riechert 1998, 1999; Maloney et al. 2003).

Many insecticides used to control insect pests may also affect spider populations either directly (through death) or indirectly (changes in behavior or physiology). Given the likely importance of spiders in insect control, researchers have evaluated pesticide toxicity for various spider species. In one major study, the susceptibility of several spiders to 30 pesticides was tested (Mansour & Nentwig 1988). Toxicity ranged from no mortality (from biological compounds, herbicides, fungicides) to medium mortality (from pyrethrins, organophosphates, catbamates), and high mortality (from cyclo compounds). Other studies have suggested that many insecticides have little effect on spider population densities (Riechert & Lockely 1984; Hilburn & Jennings 1988; VanDenBerg et al. 1990) and have led IPM researchers to rate the environmental risk of many pesticides to beneficial arthropods, in-

cluding spiders, as low (Higley & Wintersteen 1992). Other research, however, has shown that even sublethal doses of insecticides adversely affect insect (Haynes 1988) and arachnid species (Chu et al.1976; Chu et.al. 1977; Samu & Vollrath 1992).

As many insecticides affect insect reproduction to one degree or another (for example, mate location, courtship and oviposition behaviors; Haynes 1988) the present study was undertaken to investigate the effects of malathion on the mating behavior of the lycosid, *Rabidosa rabida* (Walckenaer 1837). *Rabidosa rabida* was chosen for this study because of the author's familiarity with its courtship display (Tietjen & Rovner 1982) and because of its presence in agricultural settings (e.g., Halaj et al. 2000). All tests were run using adult *R. rabida* that were laboratory-raised from antepenultimate animals captured from a grassland habitat owned by the author in Shelby County, Kentucky (USA; Location near lat. 38.21°N, long. 85.23°W). This field had not been sprayed with insecticides for at least 10 years. Spiders were tested only once and all animals were virgin. In the laboratory, spiders were housed in a manner similar to that described in Tietjen 1979. Trials were run during the 1997–2001 field seasons while analyses were performed in 2003. Data were analyzed using Stata (Stata Corporation, College Station, TX, USA).

Adult *R. rabida* were exposed to malathion or water in an 8.5 cm dia glass Petri dish with a filter paper substratum that covered the bot-

tom of the dish. Ten μl of 10^{-5} (vol %) malathion (dosed spiders) or 10 μl of distilled water (control spiders) was applied to the center of the filter paper. The appropriate concentration was determined by exposing groups of *R. rabida* males and females ($n = 10$ for each treatment) to concentrations from 10^{-3}–10^{-8} (vol %) malathion. Animals exposed to 10^{-3} and 10^{-4} malathion exhibited obvious behavioral anomalies such as difficulty in locomotion. At an exposure of 10^{-5} no such behavioral anomalies were apparent. Experimental animals were exposed to either malathion or water for 24 hr and then were tested for potential behavioral anomalies 24 hr post-exposure. This dosage technique simulates spiders walking on surfaces that have been sprayed with pesticide. No animals died when exposed to either malathion or water. For all tests I alternated between dosed and control treatments.

In the first experimental series, the effect of malathion on male courtship behavior was tested. The responses of dosed males ($n = 40$) was compared to that of control males ($n = 40$). Males were first tested for response to female pheromone by measuring latency to chemoexploratory behavior and by comparing the courtship pattern in dosed and control animals (Tietjen 1979; Tietjen & Rovner 1982).

To obtain pheromone samples, silk was collected by housing females in a standard glass Petri dish with a filter paper substratum for 24 hr. The test arena (45 cm diam.) was equipped with a paper substratum and the filter paper disk (8.5 cm diam. with a female's silk) was placed in the center. A male was then introduced near the edge of the arena and his behavior was videotaped for 10 min. Between trials, the arenas were washed with water, then 70% ethanol and allowed to air dry. The paper substratum and filter paper with silk were replaced between runs.

The responses of dosed males to a substrate with female pheromone differed from that of control males. The latency for discovering the pheromone cue and beginning palpal chemoexploratory behavior was longer for control males (6.5 min ± 6.29 SD) than for dosed males (2.6 min ± 5.57 SD; $P < 0.007$, Mann-Whitney Test). This result can be explained by the elevated activity of dosed males, which allowed them to contact the silk stimulus sooner than control animals (Tietjen, unpub-

lished data). Once control males contacted and explored the pheromone source they switched to courtship behavior faster than dosed males (control: 1.1 min ± 1.97 SD; dosed: 1.8 min ± 1.73 SD; $P < 0.01$, Mann-Whitney Test).

In order to compare courtship behavior, videos of the male's courtship behavior were digitized at 10 frames per second and examined using a proprietary computer program. First-leg tapping and palpal rotation sequences were analyzed by examining the time between palpal rotations, the time between first leg taps, and the overall symmetry of behavior (i.e., switching between left and right limbs). No differences in the timing or symmetry of the palps or first leg movements were observed between the control and dosed males ($P > 0.05$, Mann-Whitney Test for each analysis).

Following the exposure of males to a female's silk, the responses of the males to normal females was examined by immediately transferring them to a second arena that was prepared as described for the chemoexploratory tests. They were allowed 10 min to acclimate before a female was introduced as far as possible from the test male. Trials were run for an hour or until the spiders stopped copulating.

Males of both treatments courted in response to females, but when females indicated readiness to mate with a first-leg wave, dosed males did not approach the female. Instead, all the dosed males either retreated from the female only to begin courtship again, or would simply continue courting. On the other hand, 38 of the 40 control males mated within 20 min and the remaining males successfully mated within 45 min. Thirty eight of the dosed males that ignored the female's mating signal were attacked and killed. Only two dosed males eventually mated at 42 and 48 min after the female's introduction into the arena. It is interesting to note that the effect of malathion on the spiders' nervous system was very specific and only affected the transition from courtship to mating behavior and not the timing or symmetry of the courtship sequence. Females were not tested to determine if ingestion of malathion-exposed males affected their behavior.

In a second experimental series the responses of dosed and undosed females to a standard male stimulus were explored. The test arena

for females was a rectangular glass container with a 20 × 15 cm floor area. This arena replaced the circular arena used for testing male responses because the flat walls would not distort the video playback of a courting male that was used as a stimulus for the females.

The standard male stimulus was generated by videotaping a single male's courtship dance in response to a female's silk. Males were videotaped in the same arena used for testing females. The camera angle was adjusted so it would be similar to a female's view of a courting male on a flat surface. A speaker in contact with and under the floor of the arena served as a microphone to record the courtship vibrations.

The resulting 48 sec sequence was digitized at 30 frames per second and prepared so it would play in a continuous loop. The video was presented to the female along one of the 15 cm wide arena walls and was adjusted to approximate the size of a typical male. Courtship vibrations were played back using the speaker positioned under the floor of the females' test arena so that females were exposed to both visual and vibrational components of a standard male courtship display (silk from males was not introduced). These precautions eliminated variations in male courtship response as a confounding factor in the analysis. The false bottom of the test arena had a one-cm grid to facilitate distance measurements.

Females ($n = 20$) were individually introduced into the test arena and allowed 10 min to acclimate before the video was played. Tests ran for 10 min, The arena was washed and the substratum was replaced between runs. As before, the runs were videotaped and digitized at 10 frames per second for later analysis.

The time for the female to turn and face the screen and her distance from the screen were recorded as well as when she first touched the screen, attacked the screen, or had no response. Fifteen of the 20 control females and 17 of the dosed females responded to the video. For animals that responded, there were no differences between the control and dosed animals for times to face the screen, first touch, or attack ($P > 0.05$, Mann-Whitney test for each test). The apparent lack of an effect on female behavior can be explained since this test only assayed the female's participation in courtship. Thus, if the female's response to the

pesticide is similar to that the male's, we would expect her courtship behavior to be unaffected (males showed normal courtship but couldn't switch to mating).

In the third experimental series, fresh males and females were dosed with malathion and their responses were compared to normal pairs. Twelve pairs for each treatment were observed for 60 min trials. The circular arenas used for testing the responses of dosed males were used in these trials and were cleaned and prepared as before.

Males were introduced first into the arena and allowed 10 min for acclimation. Females were then introduced and the recordings began immediately. All 12 of the control males began courting the female in 8.3 min ± 8.2 SD while only 9 of the dosed males courted the females (14.5 min ± 17.4 SD). The time until courtship started did not differ between the two treatments ($P > 0.05$, Mann-Whitney Test). Mating success differed between the two groups. Only one of the control pairs failed to mate compared to seven of the dosed pairs ($P < 0.05$, Chi Square Test). The mean time to copulation for control spiders was 12.4 min ± 9.7 SD while dosed spiders took 27.7 min ± 20.8 SD to accomplish the task.

This study indicates that a single dose of a neurotoxic pesticide interferes with the mating behavior of both male and female *R. rabida* and it suggests several areas for future research. The effects of chronic exposure and the possible persistence of behavioral anomalies deserve further attention, along with studies comparing potential fitness consequences for spiders from different families or with dissimilar feeding and mating strategies. A variety of other pesticides including other neurotoxins, hormone disruptors, biocontrol agents, herbicides and fungicides should also be examined to determine if sublethal exposure affects the behavior or reproductive physiology of spiders. These data suggest that the behavioral effects of pesticide exposure should be considered by future researchers.

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SYMBIOTIC RELATIONSHIPS BETWEEN PSEUDOSCORPIONS (ARACHNIDA) AND PACKRATS (RODENTIA)

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ABSTRACT. Thirty-two species of pseudoscorpions have been found co-existing with nine packrat (or woodrat) species of the genus *Neotoma*, and this association has been referred to as phoresy. Phoresy is a term for passive dispersal when an animal literally hitches a ride on another to reach a new habitat. The pseudoscorpions reported above live in or on the nests of the packrats and do not ride on the rats themselves, eliminating a truly phoretic association. All life-history stages of the small arachnids have been found in packrat nests, indicating at least a commensalistic relationship exists, whereby the pseudoscorpion benefits from shelter and food found in the nests, and reproduces there as well. Two pseudoscorpion species have been reported feeding on packrat ectoparasites, specifically larval and adult fleas, and thus a mutualistic relationship beneficial to both "guest" and "host" exists.

RESUMEN. Treinta y dos especies de pseudoescorpión han sido halladas en los nidos de ratas del género *Neotoma*, y esta asociación ha sido llamada foresis. Foresis, sin embargo, es un término específico para dispersión pasiva donde un animal viaja sobre otro para llegar a un nuevo habitat. Los pseudoescorpiones viven en los nidos de las ratas y no han sido encontrados sobre las ratas mismas, descartando una verdadera asociación foretica entre ellos. En los nidos de las ratas se han encontrado todos los estadíos del ciclo de vida de los pseudoescorpiones, indicando que existe una asociación comensalistica donde los pequeños arácnidos se benefician de la protección y el sustento que reciben en el nido, e incluso se reproducen en él. Se han reportado dos especies de pseudoescorpión alimentandose de los ectoparasitos de las ratas, específicamente de pulgas larvales y adultas, resultando en una asociación mutualistica donde ambos el "huesped" y el "hospedero" se benefician.

Keywords: Packrats, *Neotoma*, phoresy, commensalism, mutualism

The presence of pseudoscorpions in rodent nests has been known for a long time (e. g., see Beier 1948; Weygoldt 1969). Noteworthy are the interactions between these arachnids and packrats (also known as woodrats) of the genus *Neotoma* Say and Ord, 1825; to date, 20 genera and 32 species of pseudoscorpions have been registered from the nests of 9 species of packrats. A number of these reports came from faunistic surveys of the nest inhabitants (e. g., Walters & Roth 1950; Beck et al. 1953; Fitch & Rainey 1956; Cudmore 1986; and Alvarez et al. 1988), which merely list the arthropods found on or inside the packrat nests. A number of other reports originate from taxonomic works describing the often-new species of pseudoscorpions retrieved from those nests (Chamberlin 1952; Hoff & Clawson 1952; and Hoff 1956a, b, c), paying little attention to the possible interactions between "host" and "guest".

Symbiosis has been defined by Wilson (1975) as the intimate, relatively protracted, and dependent relationship of members of one species with those of another. He further recognized three kinds of such interactions: parasitism, commensalism and mutualism. Phoresy is defined as "A symbiotic relationship, especially among arthropods and some fishes, in which one organism transports another organism of a different species" (http://www.yourdictionary.com/). Vachon (1940) provided the first comprehensive review of the topic of phoresy in pseudoscorpions. He noted that

many different species had been reported clinging to the appendages of other arthropods, primarily flies (Diptera), presumably for dispersal to new habitats, and termed it active phoresis. Other pseudoscorpions have been found as "residents" under the wing-covers or elytra of beetles (Coleoptera), presumably feeding on mites (ectoparasitic and/or ecto-commensalistic) and not readily engaged in dispersal activities, and he termed this passive phoresis. He also noted that some pseudoscorpions had been retrieved from the plumage of birds, and presumed that they were feeding on feather mites (Acari), and thus also fell under his category of passive phoresis. In light of the various definitions given above, active phoresis is an example of commensalism where the pseudoscorpion benefits from being dispersed, and the fly is neither harmed nor benefited. Passive phoresy however could be either an example of ectocommensalism where the pseudoscorpion benefits both from the protection afforded by the elytra of the beetle and from the nourishment on non-parasitic mites while there, and the beetle gets no benefits; or an example of mutualism if the pseudoscorpion feeds on parasitic mites thus benefiting the beetle by their removal.

Beier (1948) elaborated upon Vachon's review; he restricted phoresy to mean Vachon's active phoresy and coined the term phagophilia (= "love to eat") for his passive phoresy based on the assumption that the pseudoscorpions "ride" their hosts to feed upon the commensals and ectoparasites. The terms ectocommensalism and ectoparasitism are currently favored over phagophilia. In the same paper Beier also discussed four other kinds of associations between pseudoscorpions and other animals: (a) species found in the nests of social insects, (b) species found in bird nests, (c) species found in the nests of small mammals or on such mammals, and (d) species found in human habitations. This was an unfortunate classification, because given the title of Beier's paper, ever since then the interaction between pseudoscorpions and packrats has been regarded as phoretic in nature and not given further consideration, even though the pseudoscorpions are not riding on the rats for dispersal purposes.

Finally, Muchmore (1971) updated Beier's work, providing additional records primarily from the New World and from his own ob-

servations. In this work he followed Beier's classification, and made a remark that further detracted from establishing the true nature of the interactions between pseudoscorpions and packrats: "Because all of the species listed above (of pseudoscorpion) belong to genera whose members typically inhabit soil and ground litter, it is reasonable to believe that their associations with mammals come about by chance." Chamberlin (1952) described three new species, from three different genera, then known only from *Neotoma* nests. Hoff & Clawson (1952) described five new species in four different genera, from *Neotoma* nests. Hoff (1956b) described one new genus and four new species from *Neotoma* nests. Are these discoveries the result of "fortuitous" associations? Could Knudsen's (1956) findings of 1 to 44 pseudoscorpions in 109 out of 153 (71%) nests sampled come about by "chance"? Does the diversity of pseudoscorpion taxa found *in* the nests of several different species of *Neotoma*, not *on* the rat itself, support the notion of phoresy? In this contribution we review the existing information on pseudoscorpion-packrat associations and propose that they are commensalistic and/or mutualistic rather than phoretic in nature.

MATERIALS AND METHODS

A typical packrat nest has four separate components (Álvarez et al. 1988). (1) The cover (= "the hut", "the house" or "the midden") which consists of sticks, prickly-pear pads and other assorted objects (bones, plastic toys, etc.) topping the nest. (2) The green chamber (= "feeding chamber") where the rat stores and eats its food, consisting primarily of fresh vegetable matter, fungi, fruits and seeds. (3) The resting chamber(s) (= "nest cups" or "the inner nest") consisting primarily of dried grass and fur. (4) The passages that interconnect the other components. The exact composition, size and quality of the materials used in the various parts of the nest vary among individuals and also between species (e. g., see Villegas-Guzman, 2003). Each component offers a different environment for small arthropods and differs in its accessibility to them from the surrounding areas.

Two recent contributions have actually searched for pseudoscorpions in different parts of the packrat nests (Montiel-Parra & Villegas-Guzman, 1997; and Villegas-Guz-

man 2003). These two studies reveal trends of frequency (i. e., percentage of nests of a given species of packrat occupied by a given species of pseudoscorpion), density (i.e., number of individuals of a given species of pseudoscorpion, including different life history stages found in a given nest), and diversity (i. e., number of species of packrats whose nests are inhabited by the same species of pseudoscorpion). In addition, knowledge of the location of the pseudoscorpion on or in the nest provides some insight into the possible interactions between "host" and "guest".

A single specimen of leaf-litter or bark inhabiting pseudoscorpion found on the cover of a packrat nest suggests nothing more than accidental transportation on a stick carried by the rat to build-up and maintain its nest—this is an incidental association due to chance. One or more pseudoscorpions of the same species, in the green chamber of several nests of the same species of packrat would indicate that they actively seek, and remain in, this habitat to feed upon scavengers and detritivores (mostly mites)—this is commensalism. Finding many pseudoscorpions, including all or most life-history stages (depending on the season of sampling) inside the nest implies a more intimate association, and if the pseudoscorpions are feeding on fleas (both larvae and adults) or parasitic mites found in the resting chamber, then we have mutualism.

In the first study, Montiel-Parra & Villegas-Guzman (1997) excavated five nests of the packrat *N. albigula* Hartley, in a pine forest in Durango, Mexico.

In the second study Villegas-Guzman (2003) sampled the following packrat nests: ten nests of *N. albigula*, five in Tamaulipas and five in San Luis Potosi, Mexico, in dry xerophytic scrubland; seven nests of *N. palatina* in Zacatecas, Mexico, in low deciduous forest; five nests of *N. goldmani* in San Luis Potosi, Mexico, associated with prickly-pear plants (*Opuntia* sp.) in dry scrubland; five nests of *N. mexicana* in mixed oak-pine forest in Durango, Mexico; and five nests of *N. micropus* in thorn bush in Tamaulipas, Mexico. In each study the various components from each nest were collected into separate plastic bags, and returned to the laboratory for processing. The samples were initially weighed and hand-sorted in search of arthropods; and subsequently placed individually in Berlese

funnels for one week to extract the fauna therein. The remaining nest materials were hand-sorted a second time to ensure thorough collections. The pseudoscorpions obtained were processed following Hoff's (1949) method, with the modifications recommended by Wirth & Marston (1968). The specimens are deposited in the Colección Nacional de Arácnidos (CNAN) of the Instituto de Biología, Univ. Nacional Autonoma de México. Further details are given in Villegas-Guzman & Perez (2005).

RESULTS

Walters & Roth (1950) used Berlese funnels to sample the fauna of the "inner nest" (n=30) of *N. fuscipes monochroura* Rhoads near Corvallis, Oregon, and reported that ". . . pseudoscorpions . . . were found commonly in all the nests," but no further details on density and abundance were given, and the species was subsequently described as *Dinocheirus serratus* (Moles 1914). In the description of *D. sicarius* Chamberlin 1952 (Chamberlin 1952) [the records in the literature appear as *D. sicarius* but Muchmore (1997) synonymized this name under *D. serratus*] are listed five males from a nest of *N. fuscipes* found in Berkeley, California; and the following are listed from three nests (both "nest house" and "midden" reported separately) of *Neotoma* sp. from Monterey, California [nest 646: 6 ♀♀, 28 NN (=nymphs); nest 647: 1 ♂, 8 ♀♀, 20 NN; nest 649: 1 N]. Here we have the first evidence that the pseudoscorpions are apparently not only living in, but also reproducing inside the packrat nests.

Beck et al. (1953) sampled the "inner nest" of two species of packrat in Utah. In three out of 16 nests surveyed of *N. cinerea* (Ord) they reported seven specimens of *Archeolarca rotunda* Hoff & Clawson 1952; although in the original description of that species the authors provide records from five different nests, as follows: (a) March 1951: 2 ♂♂, 3 ♀♀, 1 T (=tritonymph); (b) March 1951: 1 ♀, 1 D (=deutonymph); (c) Oct.: 1 D; (d) Nov. 1951: 1 ♀; (e) Nov. 1951: 1 ♂, 3 ♀♀, 1 D. Here we have further evidence that the pseudoscorpions are actually living and reproducing inside the packrat nests. Beck et al. (1953) also reported finding 31 specimens of an "undetermined family" in 8 out of 35 nests of *N. lepida* Thomas sampled. This is presumably

Hesperochernes utahensis Hoff & Clawson 1952, and in the original description (1952) the authors report it from both *N. lepida* [April 1951: 1 ♂, 2 ♀♀, 2 TT, 1 D, 2 PP (=protonymph)] and *N. cinerea* (April 1949: 1 ♂, 2 ♀♀, 4 NN).

Knudsen (1956), in a remarkable contribution that has received little attention in the pseudoscorpion ecology literature, reported the presence of the pseudoscorpion *D. serratus* in 71% of 153 packrat nests surveyed in Los Angeles Co., California, and he found from one to 44 "guests" per nest. The pseudoscorpions fed on larval and adult fleas (Siphonaptera), as well as mites and other arthropods. During the summer months Knudsen found an average of 18 fleas in nests without pseudoscorpions, and only 12 fleas in nests with them. He also reports a ratio of 5 adult fleas to 3 pseudoscorpions, so we can estimate he found an average of 7 pseudoscorpions per nest. In laboratory experiments the pseudoscorpions fed readily on larval fleas (94 out of 100 tested), adult fleas (88 of 100) and mites (90 out of 100); when offered a choice between larval and adult fleas, 66% chose the former; between larval fleas and mites the choices were 70 versus 30%; and between adult fleas and mites, the fleas were taken 69% of the time.

Cudmore (1986) also used Berlese funnels to sample 10 nests of *N. floridana* (Ord) in Indiana. He found only one specimen of *Chthonius (Ephippiochthonius) tetrachelatus* (Preyssler 1790), and eight specimens of *Hesperochernes canadensis* Hoff 1945 in four separate nests. In those 10 nests he found 16,380 mites, belonging to 20 different species of both parasitic and non-parasitic habits.

Montiel-Parra et al. (2001) found 144 specimens of *Tychochernes inflatus* Hoff 1956: 11 ♂♂, 5 ♀♀ (two carrying 12 and 13 eggs, respectively), 15 TT, 75 DD and 38 PP from five nests of *N. albigula* in Durango. Also in one of the five nests they found seven specimens (3 ♂♂, 4 ♀♀) of *Cheiridium insperatum* Hoff & Clawson 1952. This pseudoscorpion species was apparently originally discovered by Beck et al. (1953) in Utah, who reported two specimens as "new genus & new species" from two nests of *N. cinerea*; whereas Hoff & Clawson in the original description (1952) detail specimens from two nests, as follows: (a) Aug.: 3 ♀♀, 3 ♂♂, 2 TT; and (b) Sept.: 10

♂♂, 7 ♀♀, 5 TT, 1 D, 1 P. Montiel-Parra & Villegas-Guzman (1997) found 7,427 arthropods in the five nests sampled, ranging from 2906 to 266 per nest (x̄ = 1495); and their breakdown in the nest components was: 5,342 in the resting chamber (71%), 941 in the passageways (13%), 783 in the green chamber(s) (11%) and only 361 (5%) on the cover. Among the pseudoscorpions the seven specimens of *Ch. insperatum* were found in the green chamber; whereas for *T. inflatus* 110 were in the resting chambers (75%), 20 in the green chambers (14%), 10 on the cover (7%) and 6 (4%) in the passageways. They found 374 fleas (Pulicidae and Ceratophyllidae), mostly in the resting chambers. This distribution inside the nest suggests that *Ch. insperatum* probably feeds on scavengers and that *T. inflatus* feeds on ectoparasites, especially the fleas, just as *D. serratus* does in the nests of *N. fuscipes* in California and Oregon.

Finally, Villegas-Guzman (2003) found 159 pseudoscorpions belonging to 11 different species in the 32 nests of five different species of packrats studied; some nests had single specimens, others had numerous specimens. Their distribution inside the nests was as follows: 64 in the resting chamber (40%), 53 on the cover (33%), 30 in the green chamber (19%), and 12 in the passageways (8%). Additional details can be found in Villegas-Guzman & Perez (in press). Six of the eleven species recorded by Villegas-Guzman (2003) can be regarded as incidentals, having been carried to the nest by the rat with some food or nest material, unknown to both the pseudoscorpion and the rat. One female of *Lustrochernes grossus* (Banks 1893) was found in the resting chamber of a *N. albigula* nest. One female *Paraliochthonius* sp. was found on the cover of a *N. mexicana* nest. One female of *Serianus dolosus* Hoff 1956 was found in the green chamber of a *N. albigula* nest. Two deutonymphs of *Chelifer cancroides* (L. 1758) were found on the cover of a *N. micropus* nest. Three deutonymphs of *Dinocheirus* sp. were also found on the cover of a *N. palatina* nest. Finally, *Juxtachelifer fructuosus* Hoff 1956 was found in nests of two species of rats: (a) one deutonymph in the resting chamber of a *N. albigula* nest; and (b) and three females—two in the cover and one in the green chamber—of a *N. mexicana* nest. Most likely

these pseudoscorpions were brought in during the foraging forays of the residents.

Four of the species reported by Villegas-Guzman (2003) can be considered commensalistic because of their ubiquitousness in packrat nests. First, 25 specimens of *Ch. insperatum* were found in five of the seven nests of *N. palatina* sampled; all life stages were retrieved from the nests; and individuals were found in the four separate nest components, although primarily (20) on the cover. This species was previously recorded from *N. albigula* nests from Durango by Montiel-Parra et al. (2001). Second, 16 specimens of *Illinichernes distinctus* Hoff 1949 were collected from two of the five nests of *N. mexicana*; all life stages were obtained from all the separate nests components. Third is *Larca chamberlini* Malcolm & Benedict 1978, where 18 specimens were retrieved from two nests of *N. mexicana* in Durango; all life stages except protonymphs were present (and their absence from the samples is probably correlated with the species life cycle and the season of sampling), and individuals were found in all parts of the nests. Finally, *Tychochernes inflatus* was collected from the nests of three different species of rats: (a) 22 specimens from four nests of *N. albigula* from San Luis Potosi, all life stages, mostly from the resting chambers; (b) 29 specimens from five nests of *N. goldmani*, also from San Luis Potosi; all life stages represented, mostly from the resting chambers; and (c) 10 specimens from one nest of *N. mexicana*, from Durango; only adults, but also mostly from the resting chamber. It is noteworthy to recall that 144 specimens of *T. inflatus* were also recovered from five nests of *N. albigula* from Durango; all life stages represented, and also primarily from the resting chambers (Montiel-Parra et al. 2001).

Lastly, the specific nature of the symbiotic relationship between *Pachychernes* sp. and *N. micropus* is more difficult to ascertain. This undescribed species is known only from 23 specimens (1 ♂, 3 ♀♀, 11 TT, 5 DD, 3 PP) collected in four of the five nests sampled; however, all specimens were on the "cover" of the nests except for one tritonymph found in the "green chamber". The nesting habits of this packrat differ from other species in usually lacking passageways and green chambers; the nests have a well defined resting chamber (occasionally 2), and the materials usually as-

sociated with the green chamber, such as mesquite pods and seeds, were mixed with the lower half of the cover (moist and rotting sticks). Their absence in the resting chamber strongly suggests that they do not feed on the rats' ectoparasites, and thus they should be considered as strict commensals.

All the available records of pseudoscorpion-packrat coexistence are listed in Table 1, and the most important conclusions are summarized below. A total of 32 species of pseudoscorpion have been found coexisting with nine packrat species, and of these, 8 species are known only from those nests! The rat hosting the greatest number of pseudoscorpion species is *N. albigula* with eight species, followed by *N. mexicana* and *N. micropus* with five species each. The pseudoscorpion with the most "hosts" is *Tychochernes inflatus*, found in nests of four different packrats, followed by *Archeolarca rotunda*, *Ch. insperatum* and *Hesperochernes molestus* Hoff 1956, each found coexisting with three *Neotoma* species. Pseudoscorpions of the genus *Dinocheirus*, belonging presumably to seven different species (the two unidentified specific records were found coexisting with different species of packrat than the five identified species), coexist with packrats, as do four different species in the genus *Hesperochernes*.

There are 17 taxa which have been reported only once, from a single nest. Of these, 10 are represented by single specimens, even though on some of them more than one nest was sampled: *Chthonius tetrachelatus*, one specimen from 10 nests; and *Lustrochernes grossus*, *Paraliochthonius* sp. and *Serianus dolosus*, one specimen in five nests each. Two pseudoscorpion species are represented by two individuals, and for one of these, five "host" nests were sampled; two additional species are known from three specimens, one of them also from multiple nest sampling; and one species is represented by four specimens from a single nest. These occurrences we accept as due to chance, and consider the "coexistence" to be merely incidental. However, there are two other single-nest records that indicate another type of interspecific interaction: for *D. imperiosus* Hoff 1956, 14 specimens were found in one nest, and for *D. venustus* Hoff & Clawson 1952, 61 specimens in a single nest!

Table 1.—Pseudoscorpions recorded from packrat nests, including number of nests sampled, number of nests in which pseudoscorpions were found, life stages present (MM = males, FF = females, TT = tritonymphs, DD = deutonymphs, PP = protonymphs), total numbers retrieved from the nests, and the citation for each record (including multiple records for either guest or host species). *Species found exclusively in Neotoma nests.

Pseudoscorpion species	Neotoma host	Nests sampled	Nests having pseudo-scorpions	MM	FF	TT	D	PP	Total found	Authors
Aglaochira rex* Chamberlin 1952	sp.	?	1		1				1	Chamberlin, 1952
Archeolarca rotunda	cinerea	?	5	3	8	1	3		20	Hoff & Clawson, 1952
	cinerea	?	3						7	Beck et al., 1953
	albigula	?	1		4	2			6	Hoff, 1956c
	sp.	?	?	2	3	3 nymphs			8	Muchmore, 1971
Atemnidae	sp.	?	?		1	2 nymphs			3	Muchmore, 1971
Cheiridium insperatum*	cinerea	?	2	4	10	7	1	1	23	Hoff & Clawson, 1952
	albigula	5	1	3	4				7	Montiel-Parra et al., 2001
	albigula	5	1	3	5				8	Villegas-Guzmán, 2003
	palatina	7	5	7	9	4	4	1	25	Villegas-Guzmán, 2003
Chelifer cancroides	micropus	5	1				2		2	Villegas-Guzmán, 2003
Chthonius tetrachelatus	floridana	10	1						1	Cudmore, 1986
Dinocheirus astutus Hoff 1956	albigula	?	19	17	28	65 nymphs			110	Hoff, 1956a
	sp.	?	1	1	1				2	Hoff, 1956a
Dinocheirus imperiosus*	sp.	?	1			13 nymphs			14	Hoff, 1956a
Dinocheirus texanus Hoff & Clawson 1952	micropus	?	2	5		5 nymphs			10+	Hoff & Clawson, 1952
Dinocheirus serratus	fuscipes	30	all						many	Walters & Roth, 1952
	fuscipes	?	?	5					5	Chamberlin, 1952
	fuscipes	153	109	1 to 44 per nest					many	Knudsen, 1956
	sp.	?	1	1	3				4	Muchmore, 1971
	sp.	1	1	6	9	6 nymphs				Muchmore, 1997
	sp.	1	1	1						Muchmore, 1997
	sp.	1	1	1	3	4 nymphs				Muchmore, 1997
	sp.	1	1	7	5	4 nymphs				Muchmore, 1997
Dinocheirus venustus	sp.	?	1	8	33	20 nymphs			61	Hoff & Clawson, 1952
Dinocheirus sp.	cinerea	?	1						1	Beck et al., 1953
Dinocheirus sp	palatina	5	1				3		3	Villegas-Guzmán, 2003
Hesperochernes canadensis	floridana	10	4						8	Cudmore, 1986
Hesperochernes molestus*	sp.	?	1	3	1	14 nymphs			18	Hoff, 1956a
	albigula	?	1	1					1	Hoff, 1956a

Table 1.—Continued.

Pseudoscorpion species	Neotoma host	Nests sampled	Nests having pseudo-scorpions	MM	FF	TT	D	PP	Total found	Authors
Hesperochernes unicolor (Blanks 1908)	micropus	?	1		1				1	Hoff, 1956a
Hesperochernes utahensis	micropus	?	1	1	1				2	Hoff & Clawson, 1952
	cinerea	?	1	2	2	4 nymphs			7	Hoff & Clawson, 1952
	lepida	?	1	1	2	2	1	2	8	Hoff & Clawson, 1952
Illinichernes distinctus	mexicana	5	2	5	4	1	6		16	Villegas-Guzmán, 2003
Juxtachelifer fructuosus*	albigula	5	1				1		1	Villegas-Guzmán, 2003
	mexicana	5	1	1	2				3	Villegas-Guzmán, 2003
Larca chamberlini	albigula	18		19	22	50 nymphs			91	Hoff, 1956b
	mexicana	5	2	4	5	8	1		18	Villegas-Guzmán, 2003
Lechytia hoffi Muchmore 1975	lepida	?	1						1	Beck et al., 1953
	lepida	?		1					1	Hoff & Clawson, 1952
	albigula	?		4	2				6	Hoff, 1956c
Lustrochernes grossus	albigula	5	1		1				1	Villegas-Guzmán, 2003
Microbisium parvulum (Banks 1895)	sp.	?	1		1				1	Muchmore, 1971
Globocreagris nigrescens* (Chamberlin 1952)	sp.	?	2	3	2				5	Chamberlin, 1952
Micocreagris sp.	sp.	?	1	1					1	Muchmore, 1971
n. gen. & n. sp.	cinerea	?	2		2				2	Beck et al., 1953
Paraliochthonius sp.	mexicana	5	1		1				1	Villegas-Guzmán, 2003
Pachychernes sp.*	micropus	5	4	1	3	11	5	3	23	Villegas-Guzmán, 2003
Pseudogarypinus frontalis (Banks 1909)	sp.	?	1	1					1	Muchmore, 1971
Pseudozaona sp.	sp.	?	1		1	3 nymphs			4	Muchmore, 1971
	sp.	?	1	1					1	Muchmore, 1971
Serianus dolosus	albigula	5	1		1				1	Villegas-Guzmán, 2003
Tychochernes inflatus*	sp.	?	1	1					1	Hoff, 1956a
	albigula	5	5	11	5	15	75	38	144	Montiel-Parra et al., 2001
	albigula	5	5	13	22	13	66	30	144	Villegas-Guzmán, 2003
	albigula	5	4	3	1	6	11	1	22	Villegas-Guzmán, 2003
	goldmani	5	5	4	5	12	7	1	29	Villegas-Guzmán, 2003
	mexicana	5	1	4	2	?	?	?	6	Villegas-Guzmán, 2003

DISCUSSION

First, it is important to note that there are no reports of pseudoscorpions on packrats, ruling out phoresy as the primary association between these organisms. It is not only possible, but also quite probable, that the pseudoscorpions engaged in a commensalistic/mutualistic association with packrats use phoresy as a means of dispersal between host nests. There are reports of pseudoscorpions on other mammals and those specific instances mostly are indeed phoresy, although in the case of *Epichernes aztecus* Hentschel (in Muchmore & Hentschel 1982), a more intricate interaction seems to be going on (see below).

The presence of those pseudoscorpion species found in more than one nest, coexisting with more than one packrat species, or represented by adults and nymphs inside the nests cannot be due to chance alone. We consider that the interaction between packrats and pseudoscorpions is clearly mutualistic in the case of *D. serratus*, which is not only known to feed on adult and larval fleas, but also caused an important reduction in flea numbers inside the hosts' nests (from an average of 18 to an average of 12; Knudsen 1956); and possibly so in the case of *Tychochernes inflatus* because of its prevalence in the resting chambers of the nests, the diversity of packrat species it coexists with, and the single observation of an adult feeding on a flea larva (Montiel-Parra et al. 2001). All the other species, for the time being, are here considered commensalistic due to lack of information regarding their feeding habits—if they are shown to feed, even occasionally, on the rats' ectoparasites (mites and fleas primarily) then they would become mutualists. In either case, the benefits of this association to the pseudoscorpions are multiple: (a) the nests provide protection from the weather; (b) they also provide a more benign microclimate, especially in the arid and semiarid regions inhabited by packrats; and (c) due to the packrats' habits of feeding inside the nest, a community based on scavengers and detritivores develops on which the pseudoscorpions prey [see Montiel-Parra and Villegas-Guzman (1997), for an analysis of the trophic structure of a nests' arthropod community].

The diversity of mammalian nests inhabited by pseudoscorpions goes beyond packrats and has been reported from several continents (Weygoldt 1969; Muchmore 1971); if those mammals do not feed in their nests, then the pseudoscorpions are most likely feeding on ectoparasites, thus establishing a mutualistic relationship. The number of pseudoscorpion species known exclusively or primarily from packrat nests keeps increasing as these microhabitats are adequately sampled, and this attests to the suitability of the nests as an environment conducive to reproductive success. We predict that additional pseudoscorpion species will be discovered as more mammalian nests are sampled adequately.

From an evolutionary perspective it is not difficult to envision how these associations develop. First, a rodent brings material into its nest, be it food or bedding material (e.g., straw) and accidentally transports the pseudoscorpion along. Finding a suitable environment and an adequate food supply the pseudoscorpions have no pressing need to leave and stay as commensals. If necessary, the pseudoscorpions can leave the nests either actively, by walking out, or passively, by riding on the rodent during one of its foraging expeditions (= phoresy). How do the pseudoscorpions colonize new nests? Accidentally, as in the opening scenario, or by hitching a ride directly to their new home when offspring rodents disperse from the maternal nest (again = phoresy). It is well documented that rodents, and rodent nests, have arthropod ectoparasites that are suitable pseudoscorpion prey, and thus the transformation from commensal to mutualist is uneventful and evolutionarily rather simple to achieve.

Some pseudoscorpions are apparently obligate rodent-nest inhabitants, but it is not presently known whether they have a commensalistic or a mutualistic relationship with their host(s), as is the case of the European *Lasiochernes pilosus* (Ellingsen 1910), which is known only from vole (*Microtus* spp.) and mole (*Thomomys* spp.) nests and has never been found in leaf-litter, under tree bark or under stones (Weygoldt pers. comm.). It is quite difficult to ascertain if some of the pseudoscorpion-packrat associations are obligatory or not: although some species ($n = 8$) such as *Pachychernes* sp. from Tamaulipas are at present known only from packrat nests, no serious efforts to collect them elsewhere have been made and thus their presence outside the

nests cannot be ruled out. Pseudoscorpion species found in nests of more than one packrat species, such as *Tychochernes inflatus*, or those with wide geographical distributions, indicate dispersal activities (active or passive) contrary to an obligatory symbiotic association.

There are, however, pseudoscorpions that are found exclusively on their rodent hosts, as is the case of the genus *Epichernes* Muchmore, which has three species known only from rodents: *E. aztecus* on the volcano mouse *Neotomodon alstoni alstoni* Merriam in the vicinity of Mexico City (Muchmore & Hentschel 1982); *E. navarroi* Muchmore 1990 on the forest spiny pocket mouse *Heteromys gaumeri* Allen & Chapman, and on the white-footed mouse *Peromyscus yucatanicus* Allen & Chapman, in Quintana Roo, Mexico (Muchmore 1990); and *E. guanacastensis* Muchmore 1992 on the spiny pocket mouse *Liomys salvini* (Thomas) in Costa Rica (Muchmore 1992). Muchmore & Hentschel (1982) reported 766 specimens of *E. aztecus* combed from the fur of live-trapped mice, and the pseudoscorpions apparently feed primarily upon the ectocommensal mites which also occur on the volcano mice in large numbers. The evolutionary step from nest commensal/mutualist to mouse commensal/mutualist is small indeed, and this relationship certainly is not simple phoresy. Interestingly, *Neotomodon*, as the name implies, is closely related to *Neotoma*; and *Epichernes* is closely related to *Cheiridium*, a well-known rodent nest inhabitant, suggesting an interesting co-evolutionary scenario that deserves further investigation, and which definitely indicates that pseudoscorpion-rodent interactions are not casual or accidental.

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AN ANNOTATED CHECKLIST OF CONTINENTAL NORTH AMERICAN SOLIFUGAE WITH TYPE DEPOSITORIES, ABUNDANCE, AND NOTES ON THEIR ZOOGEOGRAPHY

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ABSTRACT. A checklist of North American solifugae is presented along with their type localities, location of types, known numbers of specimens of each sex collected and the biomic distribution of each species. One hundred ninety-six solifugid species have been recorded in mainland North America, mostly from the United States. Forty-eight species are known from types only. Fifty-five species are known from males only and twenty-four are known from females only. The large hot deserts, Chihuahua and Sonora, contain the majority of collected solifugid species.

Keywords: Solifugids, wind spiders, sunspiders, checklist, biomes, distribution, type depositories.

Muma's (1976) privately published review of solifugid families of the world included an annotated checklist of Western Hemisphere solifugid species. Since that time there have been several publications describing new species, synonymies and group revisions of this arachnid taxon in North America (Brookhart & Muma 1981, 1987; Vázquez 1981; Muma 1986/1987 (Muma published the same article in both years with different publishers); Muma & Brookhart 1988; Muma 1989; Brookhart & Cushing 2002, 2004). Harvey's (2003) monumental publication brings up to date the taxonomic status and to some extent the general distribution of solifugids worldwide. Although he refers to Muma's system of classification, Harvey does not include the species groups as used by Muma (1951, 1970, 1989) in his work on Western Hemisphere solifugids. Harvey denotes the type locality but not the type repository. The general distribution of solifugids is given in terms of geopolitical areas, i.e. provinces, states, etc. but not in the more significant biomic realm.

In addition, a zoogeographic paper written but not published by Martin Muma shortly before his death was given to the authors. In this paper Muma attempted to identify the locality of collected, identified solifugids in terms of generally accepted biomes or smaller biotic areas. He also noted the number of specimens collected as determined by the literature and his own personal experience while examining materials from museum collections and from private collections. He attempted to enumerate species as abundant, common, uncommon or rare. We have listed the exact number known when less than 10, used "several" when the number is from 10–20 and "numerous" when more than 20 specimens of a species have been recorded.

This is an attempt to clarify the fine work of Muma and Harvey and isolate the present systematic state of the Solifugae of North America as well as including zoogeographical data from the work of the late Martin Muma augmented by the subsequent work of the authors. It is hoped that this information will be of use to those involved in the studies of solifugid taxonomy, systematics, ecology and biogeography. We have cited the original publications describing the taxonomy of each species. The reader is referred to Harvey (2003) for a complete list of publications citing each species.

Twelve families of Solifugae are found worldwide, two of them in North America, the Eremobatidae and the Ammotrechidae. The Eremobatidae are divided into the subfamilies Eremobatinae and Therobatinae. At the time

of Muma's 1976 publication the continental North American solfugid fauna consisted of the Eremobatinae with three genera, 44 species, and 12 unplaced species. The subfamily Therobatinae contained four genera and 46 species. The Ammotrechidae consisted of five subfamilies of which only two were found in continental North America, the Ammotrechinae and the Saronomoinae. The North American Ammotrechinae included four genera and 17 species while the Saronomoinae had but one genus with three species. We did not include those species that are considered *nomen dubia*.

Extensive solifugid population studies have been conducted at various locations in the United States (Muma 1963; Allred & Muma 1971; Brookhart, 1972; Muma 1974a, 1974b, 1976, 1979, 1980; Brookhart & Brantley 2000) mainly in the Chihuahuan Desert and the adjacent grasslands. In addition various collecting trips were undertaken by Muma and Brookhart and by Brookhart and Brookhart in essentially the same general areas. Most of these projects utilized pitfall traps. In assessing the known number of specimens, we relied on our personal collecting data, data from examination of institutional collections and information from the literature. The abundance of immatures is not reflected in this data. Immatures are difficult to identify to species and early instars are often overlooked in examination of samples.

Solifugid environments are usually regarded as xeric and include deserts, grasslands, wind, river and beach dunes. Schmoller (1970) considered them as indicative of deserts or xeric conditions. Certain of the environments are not xeric from the standpoint of macro-habitat but may be in terms of micro-habitat, e.g. beach sand, montane or arboreal inhabitants. The zoogeographic indicators used in this article include two recognized hot deserts, Chihuahua and Sonora and have included the Sinaloan thornscrub of Brown (1994); two Cold Deserts, Mojave and Great Basin; and three arid grasslands, Interdesert grassland, Cold Dry grassland, and High Dry grassland and are based mainly on Küchler's (1985) designation. In addition, smaller biotic communities as listed by Brown (1994) and Küchler (1985) are included particularly for the state of California in the United States and also parts of Mexico.

Since most biogeographers refer to grass-lands as either short grass or tall grass a brief description of the areas included is necessary. We have relied extensively on Küchler (1985) and Brown (1994) in making these distinctions. *High Dry Grassland*: Küchler's (1985) sagebrush steppe/wheatgrass-needle grass steppe; virtually all of Colorado east of the Rocky Mountains; part of northwest Arizona; much of the northern third of New Mexico; and the northwest corner of Texas. It also includes small western pieces of Oklahoma, Kansas and Nebraska and most of the south-eastern third of Wyoming. *Interdesert Grassland:* The (Gama-tobosa shrub steppe) of Küchler (1985) including a north-south extreme western strip of New Mexico, most of Arizona north and east of the Sonora Desert, and south and east of the Mohave and Great Basin deserts, excepting perhaps part of the northwest corner of the state. *Cold Dry Grassland:* Most of Montana and Idaho, western South and North Dakota; the Columbia/Snake River Basin in Washington and Oregon; the northern one third of Wyoming; parts of the western Canadian provinces; the southwest corner of Saskatchewan, a southern strip of Alberta; and the southeastern corner of British Columbia. The California biotic communities included are the California sage; California steppe; California grassland; and California chaparral.

Type Depositories of North American Solifugae.—AMNH-American Museum of Natural History, New York, New York, USA; ANS-Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; BMNH-British Museum of Natural History, London, United Kingdom; BNHM-Boston Society of Natural History, Boston, Massachusetts, USA; BYU-Brigham Young University, Provo, Utah, USA; CAS-California Academy of Science, San Francisco, California, USA; CUM-Cornell University Museum, Ithaca, New York, USA; DEZC-Dipartimento di Entomologia e Zoologia, Turin, Italy; DMNH-Denver Museum of Nature and Science (formerly Denver Museum of Natural History), Denver, Colorado, USA; FSCA-Florida State Collection of Arthropods, Gainesville, Florida, USA; IBUNAM-Labortorio de Acarologia, Instituto de Biologia, Universidad Nacional Autónoma de Mexico, Coyoacan, D.F., Mexico; MCZ-Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA;

MNNH-Museum National d'Histoire Naturelle, Paris, France; MNRJ-Museo Nacional Rio de Janeiro, Rio de Janeiro, Brazil; NMWA-Naturhistorisches Museum, Wien, Austria; SMF-Natur-Museum und Forschungs-Instut Senckenberg, Frankfurt am Main, Germany; UCBC-University of California at Berkeley, Berkeley, California, USA; UCR-University of California at Riverside, Riverside, California, USA; USNM-United States National Museum, Washington, District of Columbia, USA; ZMHU-Zoologisches Museum der Humboldt Universität, Berlin, Germany; ZSM-Zoologisches Staatsinstitut ad Museum, Hamburg, Germany.

FAMILY EREMOBATIDAE Roewer 1934

Key to Subfamilies and Genera of Eremobatidae (males only)

(Taken from Muma 1987)

1. Leg 1 with one claw; chelicerae about twice as long as wide; small to large species . . . . .
   . . . . .Eremobatinae 2
   Leg 1 with 2 claws; chelicerae 2.5–3 times longer than wide; tiny to moderate sized species
   . . . . Therobatinae 6
2. Fixed cheliceral finger long, style-like or needle-like; mesoventral groove a crease, slot or cup-like structure; moderate-sized to large species. 3
   Fixed cheliceral finger short, sculptured and flanged; mesoventral groove a trough-like slot; moderate sized species. . . . . *Eremothera*
3. Mesoventral groove an indistinct hollow or crease that does not extend to the base of the fixed finger; anterior tooth absent . . . . *Eremorhax*
   Mesoventral groove a distinct crease, cup, or slot that may or may not extend to base of fixed finger; anterior tooth present. 4
4. Mesoventral groove short, not extending to base of fixed finger; apical striate or plumose setae of male flagellum complex not obviously modified or flattened 5
   Mesoventral groove long, extending to base of fixed finger; apical plumose seta of male flagellum complex obviously enlarged or flattened; covering part of the mesoventral groove.
   . . . . *Eremobates*
5. Palpal metatarsus, tibia, and femur provided with enlarged spine-like seta, but not robust, not aligned in a ventral row, not movable . . . . *Eremocosta*
   Palpal metatarsus, tibia, and femur provided ventrally with robust, obviously movable spine-like setae. . . . . *Horribates*
6. Fixed cheliceral finger strongly recurved, sigmoid, or S-shaped; mesoventral groove absent; both dorsal and ventral flagellum complex setae plumose, moderate sized species. . . *Chanbria*
   Fixed cheliceral finger style-like or needle-like, straight, curved, or undulate but not S-shaped or sigmoid; mesoventral groove present; dorsal flagellum complex setae striate, ventral setae striate or plumose 7
7. Fixed cheliceral finger with a mesoventral groove that may vary from a distinct crease to an elongate hollow or cup; dorsal flagellum complex simple or tubular; small to moderate sized species . . . . *Eremochelis*
   Fixed cheliceral finger without a mesoventral groove; dorsal flagellum complex hooked or spatulate; tiny to small species . . . . *Hemerotrecha*

Subfamily Eremobatinae Kraepelin 1934

Dataminae Kraepelin 1899:240.
Eremobatinae Kraepelin 1901:116.
Eremorhaxinae Roewer 1934:553 (synonymized by Muma 1951:41).

Genus *Eremorhax* Roewer 1934

Eremorhax Roewer 1934:553.
Arenotherus Brookhart & Muma 1987:3.

Eremorhax arenus
(Brookhart & Muma 1987)

Arenotherus arenus Brookhart & Muma 1987:10.
Eremorhax arenus (Brookhart & Muma): Harvey 2002:451.

Type material.—Male holotype and 4 paratype males from Palmdale, California, USA (FSCA).

Recorded specimens.—Eight males.

Distribution.—USA: California. Biome: Sonoran Desert.

Eremorhax joshui
(Brookhart & Muma 1987)

Arenotherus joshui Brookhart & Muma 1987:9.
Eremorhax joshui (Brookhart & Muma): Harvey 2002:451.

Type material.—Male holotype and female allotype from Jumbo Rocks, Joshua Tree National Monument, California, USA (FSCA).

Recorded specimens.—Numerous males and females.

Distribution.—USA: California. Biome: Mojave Desert.

Eremorhax latus Muma 1951

Eremorhax latus Muma 1951:44.
Arenotherus latus (Muma 1951): Brookhart & Muma 1987:11.
Eremorhax latus (Muma): Harvey 2002:451.

Type material.—Male holotype with no locality label (MCZ).

Recorded specimens.—Two males from southern Arizona.

Distribution.—USA: Arizona and probably Mexico. Biome: Sonoran Desert.

Eremorhax magnellus
(Brookhart & Muma 1987)

Arenotherus magnellus Brookhart & Muma 1987:5.
Eremorhax magnellus (Brookhart & Muma): Harvey 2002:451.

Type material.—Male holotype and female allotype from Lordsburg, New Mexico, USA (FSCA).

Recorded specimens.—Numerous males and females.

Distribution.—USA: New Mexico, Arizona and probably Mexico. Biome: Interdesert Grassland.

Eremorhax magnus (Hancock 1888)

Datames magna Hancock 1888:107.
Eremobates magnus (Hancock 1888): Kraepelin 1901:127.
Eremopus mexicanus Roewer 1934:564 (synonymized by Muma 1951:43).
Eremorhax magnus (Hancock): Muma 1951:43.
Arenotherus magnus (Hancock 1888): Brookhart & Muma 1987:5.

Eremorhax magnus (Hancock): Harvey 2002:451.

Type material.—*Datames magna*: Male holotype, Laredo, Texas, USA. Type deposition: unknown and type at present must be considered lost. *Eremopus mexicanus*: Male holotype from Mexico (SMF, RII/1353).

Recorded specimens.—Several males and females.

Distribution.—USA: Texas, New Mexico. Mexico: Chihuahua. Biome: Chihuahuan Desert.

Eremorhax mumai Brookhart 1972

Eremorhax mumai Brookhart 1972:3.
Arenotherus mumai (Brookhart): Brookhart & Muma 1987:6.
Eremorhax mumai Brookhart: Harvey 2002:451.

Type material.—Male holotype, Boone, Colorado, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Colorado, New Mexico. Biome: Chihuahuan Desert; High Dry Grassland.

Eremorhax pimanus
(Brookhart & Muma 1987)

Arenotherus pimanus Brookhart & Muma 1987:8.
Eremorhax pimanus (Brookhart & Muma): Harvey 2002:451.

Type material.—Male holotype from Saguaro National Monument, Pima County, Arizona, USA (FSCA).

Recorded specimens.—Five males and four females.

Distribution.—USA: Arizona, probably Mexico. Biome: Sonoran Desert.

Eremorhax puebloensis Brookhart 1965

Eremorhax puebloensis Brookhart 1965:154.
Arenotherus puebloensis (Brookhart): Brookhart & Muma 1987:4.
Eremorhax puebloensis Brookhart: Harvey 2002:451.

Type material.—Male holotype and female allotype collected at Pueblo, Colorado, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Colorado, Northern New Mexico, Northwest Texas, Northern Arizona. Biome: Chihuahuan Desert; High Dry Grassland.

Eremorhax pulcher Muma 1963

Eremorhax pulcher Muma 1963:2.
Arenotherus pulcher (Muma): Brookhart & Muma 1987:7.
Eremorhax pulcher Muma: Harvey 2002:451.

Type material.—Male holotype and female allotype, Mercury, Nevada, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Nevada, Arizona. Biome: Mojave Desert; Great Basin Desert.

Eremorhax tuttlei
(Brookhart & Muma 1987)

Arenotherus tuttlei Brookhart & Muma 1987:9.
Eremorhax tuttlei (Brookhart & Muma): Harvey 2002:451.

Type material.—Male holotype and female allotype from Yuma, Arizona, USA (FSCA).

Recorded specimens.—Ten males and three females.

Distribution.—USA: Arizona. Biome: Sonoran Desert.

Genus *Eremocosta* Roewer 1934

Eremopus Roewer 1934:561.
Eremocosta Roewer 1934:569 (type species only).
Eremocantha Roewer 1934:571.
Eremorhax Roewer 1934:553, Muma 1951:41; Muma 1970:6 (erroneously synonymized type species of *Eremocosta* with *Eremorhax*).

Eremocosta acuitlapanensis
(Vázquez & Gavino-Rojas 2000)

Eremopus acuitlapanensis Vázquez & Gavino-Rojas 2000:227.
Eremocosta acuitlapanensis (Vázquez & Gavino-Rojas): Harvey 2002:451.

Type material.—Male holotype from Acuitlapan, Guerrero, Mexico (IBUNAM).

Recorded specimens.—Two males and two females.

Distribution.—Mexico: Guerrero. Biome: Sonoran Desert.

Eremocosta bajaensis Muma 1986

Eremorhax bajaensis Muma 1986:4.
Eremocosta bajaensis (Muma): Harvey 2002:451.

Type material.—Male holotype from 3.2 km east of Rancho San Salvador, Baja California, Mexico (CAS). Female allotype from 10.2 km north of Santa Maria, Baja California, Mexico (CAS).

Recorded specimens.—Two males and one female.

Distribution.—Mexico: Baja California Norte. Biome: Sonoran Desert.

Eremocosta calexicensis (Muma 1951)

Eremorhax calexicensis Muma 1951:50.
Eremopus calexicensis (Muma): Muma 1989:6.
Eremocosta calexicensis (Muma): Harvey 2002:451.

Type material.—Male holotype, female allotype and male paratypes from Calexico, California, USA (USNM).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Arizona, California. Mexico: Baja California Norte. Biome: Sonoran Desert.

Eremocosta formidabilis (Simon 1879)

Datames formidabilis Simon 1879:136.
Datames affinis Kraepelin 1899:242.
Datames cfr. *formidabilis* (Simon): Banks 1899:378.
Eremobates formidabilis (Simon): Banks 1900:427.
Eremoperna formidabilis (Simon): Roewer 1934:561.
Eremorhax formidabilis (Simon): Muma 1970:4.
Eremopus formidabilis (Simon): Muma 1989:5.
Eremocosta formidabilis (Simon): Harvey 2002:451.

Type material.—*Datames formidabilis*: Male holotype from Guanajuato, Mexico (MNHN). *Datames affinis*: Male holotype and female allotype from Arizona, USA; No. 7297, Roewer No. 9129 (MNHN).

Recorded specimens.—Three males and a questionable record from Arkansas (probably Arizona).

Distribution.—USA: Unknown. Mexico: Guanajuato. Biome: Sonoran Desert.

Eremocosta fusca (Muma 1986)

Eremorhax fuscus Muma 1986:2.
Eremocosta fusca (Muma): Harvey 2002:451.

Type material.—Male holotype from Putla, Oaxaca, Mexico (CAS). Female allotype from 2.4 km N. Cuernavaca, Morelos, Mexico (CAS).

Recorded specimens.—Known from types only.

Distribution.—Mexico: Morelos, Oaxaca. Biotic community: Sinaloan thornshrub.

Eremocosta gigas Roewer 1934

Eremocosta gigas Roewer 1934:569.
Eremopus gigas (Roewer): Muma 1989:5.
Not *Eremorhax gigas* (Roewer 1934): Muma, 1951 (misidentification, see *Eremocosta gigasellus* (Muma 1951).

Type material.—Male holotype from Tampico, Mexico (SMF).
Recorded specimens.—Known from type only.
Distribution.—Mexico: Veracruz. Biome: Chihuahuan Desert.

Eremocosta gigasella (Muma 1970)

Eremorhax gigas (Roewer): Muma 1951:48 (misidentification).
Eremorhax gigasellus Muma 1970:8.
Eremopus gigasellus (Muma): Muma & Muma 1988:11.
Eremocosta gigasella (Muma): Harvey 2002:451.

Type material.—Male holotype from Boquillas, Texas, USA (AMNH).
Recorded specimens.—Eight males and three females (DMNH).
Distribution.—USA: New Mexico, Texas and probably Mexico. Biome: Chihuhuan Desert.

Eremocosta montezuma (Roewer 1934)

Eremopus montezuma Roewer 1934:564.
Eremorhax montezuma (Roewer): Muma 1970:6.
Eremocosta montezuma (Roewer): Harvey 2002:451.

Type material.—Male holotype from Orizaba, Mexico (NMWA, No. 8076).
Recorded specimens.—Known from type only.
Distribution.—Mexico: Veracruz. Biome: Chihuahuan Desert.

Eremocosta nigrimana (Pocock 1895)

Gluvia nigrimanus Pocock 1895:94.
Eremobates nigrimanus (Pocock): Kraepelin 1901: 128.
Eremorhax magnus (Hancock): Muma 1970:5.
Eremorhax nigrimanus (Pocock): Brookhart & Muma 1987:1.
Eremocosta nigrimana (Pocock): Harvey 2002:451.

Type material.—Male holotype labeled "Probably Meshed, Afghanistan" but the specimen may be mislabeled (see Muma, 1970:6 and Muma 1976:14) (BMNH, No. 1952).
Recorded specimens.—Known from type only.
Distribution.—Unknown. Biome: Unknown.

Eremocosta robusta (Roewer 1934)

Eremacantha robusta Roewer 1934:571.
Eremorhax robustus (Roewer): Muma 1976:15.
Eremocosta robusta (Roewer): Harvey 2002:451.

Type material.—Immature holotype from Santiago, Mexico (ZMHU, no. 996).
Recorded specimens.—Known from type only.
Distribution.—Mexico: Baja California Norte. Biome: Sonoran Desert.

Eremocosta spinipalpis (Kraepelin 1899)

Datames spinipalpis Kraepelin 1899:243.
Eremobates spinipalpis (Kraepelin): Kraepelin 1901:124.
Eremorhax spinipalpis (Kraepelin): Muma 1970:8.
Eremocosta spinipalpis (Kraepelin): Harvey 2002: 451.

Type material.—Female holotype from Santa Rosalia, Mexico (MNHN).
Recorded specimens.—Known from type only.
Distribution.—Mexico: Baja California Sur. Biome: Sonoran Desert.

Eremocosta striata (Putnam 1882)

Datames striatus Putnam 1882:255.
Datames cinerea Putnam 1882:260 (synonymized by Muma 1951:45).
Eremobates cinereus (Putnam): Kraepelin 1901: 124.
Erermorhax striatus (Putnam): Muma 1951:45.
Eremopus striatus (Putnam): Muma & Muma 1988: 10.
Eremocosta striata (Putnam): Harvey 2002:451.

Type material.—*Datames striatus*: Female holotype from Camp Grant, Arizona, USA (BNHM). *Datames cinerea*: Type locality of male holotype unknown (ANS).
Recorded specimens.—Several males and females.
Distribution.—USA: Arizona, California. Mexico: Sonora. Biome: Sonoran Desert.

Eremocosta titania Muma 1951

Eremocosta titania Muma 1951:48.
Eremopus titania (Muma): Muma & Muma 1988: 11.
Eremocosta titania Muma: Harvey 2002:451.

Type material.—Male holotype and 2 male paratypes from Twenty-nine Palms, California, USA (AMNH). Female allotype from 12 km northwest of Las Vegas, Nevada, USA (AMNH).
Recorded specimens.—Numerous males and females.
Distribution.—USA: California and Nevada. Biome: Sonoran Desert; Mojave Desert.

Genus Eremothera Muma 1951

Eremothera Muma 1951:82.

Eremothera drachmani Muma 1986

Eremothera drachmani Muma 1986:10.

Type material.—Male holotype from Nueva Guymas, Sonora, Mexico (AMNH).
Recorded specimens.—Known from type only.
Distribution.—Mexico: Sonora. Biome: Sonoran Desert.

Eremothera sculpturata Muma 1951

Eremothera sculpturata Muma 1951:82

Type material.—Male holotype from Arizona, USA, no further locality data (AMNH).
Recorded specimens.—Known from type and 3 males.
Distribution.—USA: Arizona. Mexico: Sonora. Biome: Sonoran Desert.

Genus *Eremobates* Banks 1900

Datames Simon 1879:133.
Eremobates Banks 1900:426 (in part).
Eremoperna Roewer 1934:557 (in part).
Eremopus Roewer 1934:561 (in part).
Eremocosta Roewer 1934:561 (in part).
Eremospina Roewer 1934:565.
Eremognatha Roewer 1934:569 (in part).
Eremoseta Roewer 1934:569 (in part).
Eremostata Roewer 1934:571 (in part).

Eremobates angustus group

Eremobates angustus Muma 1951

Eremobates angustus Muma 1951:80.

Type material.—Male holotype, female allotype, and male paratype from Madera Can-

yon, Santa Rita Mountains, Arizona, USA (AMNH).
Recorded specimens.—Numerous males and females.
Distribution.—USA: Arizona and Texas. Biome: Interdesert Grassland; Sonoran Desert.

Eremobates becki Muma 1986

Eremobates becki Muma 1986:7.

Type material.—Male holotype from Colonia Garcia, Chihuahua, Mexico (BYU).
Recorded specimens.—Known from type only.
Distribution.—Mexico: Chihuahua. Biome: Chihuahuan Desert.

Eremobates cruzi Muma 1951

Eremobates cruzi Muma 1951:82.

Type material.—Male holotype from Bear Valley, Santa Cruz County, Arizona, USA (MCZ).
Recorded specimens.—Three males.
Distribution.—USA: Arizona. Biome: Interdesert Grassland; Sonoran Desert.

Eremobates aztectus group

Eremobates aztecus Pocock 1902

Eremobates aztecus Pocock 1902:60.

Type material.—Male holotype and female allotype from Guanajuato, Mexico (BMNH).
Recorded specimens.—Two males and females.
Distribution.—Mexico: Guanajuato. Biotic community: Sinaloan Thornscrub.

Eremobates lapazi group

Eremobates lapazi Muma 1986

Eremobates lapazi Muma 1986:9.

Type material.—Male holotype and female allotype from 16.2 km NW of La Paz, Baja California, Mexico (CAS).
Recorded specimens.—Two males and one female.
Distribution.—Mexico: Baja California Sur. Biome: Sonoran Desert.

Eremobates pallipes group

Eremobates arizonicus (Roewer 1934)

Eremostata arizonica Roewer 1934:574.
Eremobates pallipes (Say): Muma 1951:73.

Eremobates arizonicus (Roewer): Brookhart & Muma 1981:295.

Type material.—Female holotype from Arizona, USA (ZSM). Male "allotype" from Hurley, New Mexico, USA (AMNH).
Recorded specimens.—Numerous males and females.
Distribution.—USA: New Mexico and Arizona. Biome: Interdesert Grassland.

Eremobates barberi (Muma 1951)

Eremothera barberi Muma 1951:83.
Eremobates californicus (Simon): Muma 1951:76 (in part: some males); not *Datames californicus* (Simon 1879).
Eremobates simoni Muma 1970:25 (in part: some males).
Eremobates barberi (Muma): Brookhart & Muma 1981:302.

Type material.—Female holotype from Brownsville, Texas, USA (USNM). Male allotype from Sanderson, Texas, USA (AMNH).
Recorded specimens.—Numerous males and females.
Distribution.—USA: Texas. Biome: Chihuahuan Desert.

Eremobates californicus (Simon 1879)

Datames californicus Simon 1879:143.
Eremopus californicus (Simon): Roewer 1934:565.
Eremostata californica (Simon): Roewer 1934:574.
Not *Eremobates californicus* (Simon): Muma 1951:76 (misidentification, *Eremobates simoni* Muma 1970).

Type material.—Holotype from Mariposa, California, USA is immature and cannot be properly placed (MNHN, No. 1516).
Distribution.—USA: California. Biome: Sonoran Desert.

Eremobates chihuaensis Brookhart & Cushing 2002

Eremobates chihuaensis Brookhart & Cushing 2002:87.

Type material.—Male holotype and male paratype from southeast of Chihuahua, Mexico (DMNH).
Recorded specimens.—Known from male holotype and paratype only.
Distribution.—Mexico: Chihuahua. Biome: Chihuahuan Desert.

Eremobates cinerascens (C.L. Koch 1842)

Gluvia cinerascens C.L. Koch 1842:355.
Datames cinerascens (C.L. Koch): Simon 1879:144.
Eremobates cinerascens (C.L. Koch): Kraepelin 1901:122.
Eremostata cinerascens (C.L. Koch): Roewer 1934:573.

Type material.—Male holotype from Mexico, locality unknown (MNHN, No. 9139).
Recorded specimens.—One male.
Distribution.—Mexico. Biome: unknown.

Eremobates dentilis Brookhart & Muma 1981

Eremobates dentilis Brookhart & Muma 1981:295.

Type material.—Male holotype from unknown location (AMNH).
Recorded specimens.—One male.
Distribution.—Unknown, probably Baja California, Mexico. Biome: Sonoran Desert.

Eremobates dilatatus (Putnam 1882)

Datames dilatata Putnam 1882:259.
Eremobates dilatatus (Putnam): Muma 1951:78.

Type material.—Female holotype with no locality data (ANS).
Recorded specimens.—One female.
Distribution.—Probably Baja California, Mexico. Biome: Sonoran Desert.

Eremobates dinamita (Roewer 1934)

Eremostata dinamita Roewer 1934:574.
Eremobates dinamita (Roewer): Brookhart and Muma 1981:292.

Type material.—Female holotype (labeled *Eremogyna dinamita*) from Dinamita, Durango, Mexico (MNHN, No. 8389). Muma (1970) synonymized this species with *E. pallipes*.
Recorded specimens.—One female.
Distribution.—Mexico: Durango. Biome: Sonoran Desert.

Eremobates docolora Brookhart & Muma 1981

Eremobates docolora Brookhart & Muma 1981:292.

Type material.—Male holotype from Craig, Colorado, USA (AMNH). Female allotype from southwest of Encampment, Wyoming, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Colorado, Montana, Wyoming and North Dakota. Canada: Alberta, British Columbia, Saskatchewan. Biome: Cold Dry Grassland.

Eremobates durangonus Roewer 1934

Eremobates durangonus Roewer 1934:557.

Type material.—Two female syntypes from Durango, Mexico cannot be located and must be presumed lost (Muma 1970). Brookhart and Muma (1981) did not designate a neotype because there is no specimen from type locality.

Recorded specimens.—Numerous males and females.

Distribution.—USA: Arizona, California; Mexico. Biome: Sonoran Desert.

Eremobates formicarius (C.L. Koch 1842)

Gluvia formicaria C.L. Koch 1842:356.
Datames formicarius (C.L. Koch): Simon 1879:144.
Eremobates formicaria (C.L. Koch): Banks 1900:426.
Datames formicaria (C.L. Koch): Barrows 1925:495.
Eremopus formicarius (C.L. Koch): Roewer 1934:565.

Type material.—Male lectotype from Pribla (Pueblo?), Mexico (ZMHU, No. 8335). Muma synonymized this species with *E. pallipes*.

Recorded specimens.—One male.

Distribution.—Mexico: Unknown. Biotic community: Sinaloan Thornscrub.

Eremobates gerbae Brookhart & Cushing 2002

Eremobates gerbae Brookhart & Cushing 2002:85.

Type material.—Male holotype, female allotype, and 2 males and 1 female paratype from Mack Burn Area, Rincon Mountains, Pima County, Arizona, USA (DMNH).

Recorded specimens.—Known from types, paratypes, and three males.

Distribution.—USA: Arizona. Biome: Sonoran Desert.

Eremobates lentiginosus (Kraepelin 1899)

Datames lentiginosus Kraepelin 1899:244.
Eremobates lentiginosus (Kraepelin): Kraepelin 1901:124.

Type material.—Female holotype with no locality data (Museum of Turin, Italy).

Recorded specimens.—Only known from female holotype.

Distribution.—Unknown. Biome: Unknown.

Eremobates pallipes (Say 1823)

Galeodes pallipes Say 1823:3.
Galeodes subulata Say 1823:3.
Gluvia cinerascens (Say): C.L. Koch 1842:350.
Datames pallipes (Say): Simon 1879:139.
Datames subulata (Say): Putnam 1883:267.
Eremobates pallipes (Say): Banks 1900:427.
Eremobates pallipes (Say): Fichter 1940:325.
Eremobates subulata (Say): Muma 1970:28.

Type material.—*Galeodes pallipes*: Location of the female type from Denver, Colorado, USA is unknown. Fichter (1940) established the identity of the species but did not select a neotype. Say's specimens cannot be located in North American (Muma, 1951) or European (Muma 1970) type depositories and are presumed lost. Brookhart and Muma (1981) designated a male neotype from Highway 205c, Byers, Colorado, USA and a female "allotype" from Castle Rock, Colorado, USA (AMNH). *Galeodes subulata*: The type is lost or destroyed (Muma 1951).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Colorado, Nebraska, South Dakota, Wyoming, New Mexico, Oklahoma, Texas. Biome: Chihuahuan Desert; High Dry Grassland.

Eremobates putnami (Banks 1898)

Datames putnami Banks 1898:2.
Eremobates putnami (Banks): Banks 1900:427.

Type material.—Male and young female syntypes from San Jose del Cabo, Mexico (MCZ).

Recorded specimens.—Known from types only.

Distribution.—Mexico: Baja California Sur. Biome: Sonoran Desert.

Eremobates simoni Muma 1970

Eremobates californicus (Simon 1879): Muma 1951:76 (not *Datames californicus* Simon 1879).
Eremobates simoni Muma 1970:25.

Type material.—Male holotype from Gillespie County, Texas, USA (AMNH). Female

allotype from Wichita County, Texas, USA
(AMNH).

Recorded specimens.—Numerous males
and females.

Distribution.—USA: New Mexico and
Texas. Biome: Chihuahuan Desert.

Eremobates suspectus Muma 1951

Eremobates suspectus Muma 1951:79.

Type material.—Male holotype and fe-
male allotype from White River, Arizona,
USA (AMNH).

Recorded specimens.—Numerous males
and females.

Distribution.—USA: Arizona. Biome: In-
terdesert Grassland.

Eremobates woodruffi
Brookhart & Muma 1981

Eremobates woodruffi Brookhart & Muma 1981:
302.

Type material.—Male holotype from Pul-
ligum Mountain, in Big Bend National Park,
Texas, USA (AMNH).

Recorded specimens.—Three males.

Distribution.—USA: Texas and probably
Mexico. Biome: Chihuahuan Desert.

Eremobates palpisetulosus group

Eremobates affinis (Kraepelin 1899)

Datames affinis Kraepelin 1899:242.
Eremobates affinis (Kraepelin): Kraepelin 1901:
128.
Eremoperna affinis (Kraepelin): Roewer 1934:561.
Eremobates affinis (Kraepelin): Muma & Brookhart
1988:22.
Not *Eremobates affinis* (Kraepelin), Muma 1951:65
(misidentification).

Type material.—Male and female syn-
types from Arizona, USA, no locality. No.
7297, Roewer No. 9129 (ZSM). These speci-
mens agree with Kraepelin's (1899) descrip-
tion and are therefore the types of the species.
Muma's (1970) type designation for *E. affinis*
in MNHN are not the types.

Recorded specimens.—Several males and
females.

Distribution.—USA: Arizona. Interdesert
Grassland; Chihuahuan Desert.

Eremobates ajoanus
Muma & Brookhart 1988

Eremobates ajoanus Muma & Brookhart 1988:19.

Type material.—Male holotype from south

of Ajo, Arizona, USA (FSCA). Female allo-
type from north of Organ Pipe National Mon-
ument, Arizona, USA (FSCA).

Recorded specimens.—Eight males and
seven females.

Distribution.—USA: Southwestern Arizo-
na. Biome: Sonoran Desert.

Eremobates bajadae
Muma & Brookhart 1988

Eremobates bajadae Muma & Brookhart, 1988:12.

Type material.—Male holotype and fe-
male allotype from Deming, New Mexico,
USA (FSCA).

Recorded specimens.—Numerous males
and females.

Distribution.—USA: Southern New Mex-
ico and eastern Arizona. Biome: Interdesert
Grassland.

Eremobates bajaensis Muma 1986

Eremobates bajaensis Muma 1986:5.

Type material.—Male holotype from Baja
California Norte, Mexico.(CAS). Male para-
type from Socorro Sand Dunes, Baja Califor-
nia Norte, Mexico (AMNH).

Recorded specimens.—Two males.

Distribution.—Mexico: Baja California
Norte. Biome: Sonoran Desert.

Eremobates bantai Brookhart 1965

Eremobates bantai Brookhart 1965:153.

Type material.—Male holotype and fe-
male allotype from Fremont County, Colora-
do, USA (AMNH).

Recorded specimens.—Eight males and
six females.

Distribution.—USA: South central Colo-
rado. Biome: High Dry Grassland.

Eremobates bixleri Muma & Brookhart 1988

Eremobates bixleri Muma & Brookhart 1988:21.

Type material.—Male holotype from Pima
County, Tucson, Arizona, USA (FSCA).

Recorded specimens.—Females known
from a single badly fragmented, previously
dehydrated specimen from Tucson, Arizona,
USA. Four males and one female.

Distribution.—USA: Southern Arizona,
probably Mexico. Biome: Sonoran Desert.

Eremobates coahuilanus Muma 1986

Eremobates coahuilanus Muma 1986:6.

Type material.—Male holotype from southwest of Cuatro Cienegas, Coahuila, Mexico (CAS). Male paratype from southeast of Rancho Orazco, Cuatro Cienegas Basin, Coahuila, Mexico (CAS).
Recorded specimens.—Two males.
Distribution.—Mexico: Coahuila. Biome: Chihuahuan Desert.

Eremobates fagei (Roewer 1934)

Eremopus fagei Roewer 1934:563.
Eremobates purpusi (Roewer): Muma 1951:70 (in part, males and females from Fresno and San Benito Counties, California, USA).
Eremobates villosus Muma 1970:21 (in part, males and females from Fresno and San Benito Counties, California, USA).
Eremobates fagei (Roewer): Muma 1970:16.

Type material.—Female holotype from California, USA (MNHN, Roewer No. 9134). Muma's (1951) records of *E. villosus*, under *E. purpusi*, from Pacific Grove and San Benito County may be this species.
Recorded specimens.—Several males and four females.
Distribution.—USA: California. Biotic community: California Steppe.

Eremobates girardi (Putnam 1883)

Datames girardii Putnam 1883:257.
Eremobates girardi (Putnam): Kraepelin 1901:128.

Type material.—Male holotype from Arkansas, USA (see below) was supposed to be in ANS, but has been either lost or destroyed. Not in museum in Davenport, Iowa, hometown of J.D. Putnam and J.O. Brookhart.
Recorded specimens.—Two males.
Distribution.—State of Arkansas was cited by Putnam but this is obviously in error. We have seen two males from the Sonoran region of Mexico, so Arizona would be likely location. Biome: Sonoran Desert.

Eremobates gracilidens Muma 1951

Eremobates gracilidens Muma 1951:66.

Type material.—Male holotype from Twenty-nine Palms, California, USA. Female allotype from Lone Pine, Inyo County, California, USA (AMNH).

Recorded specimens.—Numerous males and females.
Distribution.—USA: Arizona and California. Biome: Mojave Desert.

Eremobates guenini (Roewer 1934)

Eremognatha guenini Roewer 1934:567.
Eremobates guenini (Roewer): Muma 1970:17.

Type material.—Male holotype from Dinamita, Mexico (MNHN. No. 8390).
Recorded specimens.—Twelve males.
Distribution.—Mexico: Durango. Biome: Sonoran Desert.

Eremobates hessei (Roewer 1934)

Eremopus hessei Roewer 1934:567.
Eremobates hessei (Roewer): Muma 1970:18 (misidentification; see Muma 1988:8). Muma (1970) synonomized *Eremobates nodularis* Muma 1951 with *E. hessei* (Roewer 1934) and Muma & Brookhart in 1988 synonomized *E. hessei* with *E. nodularis*.

Type material.—Female holotype from Distrito Federal, Mexico (ZMHU No. 7972).
Recorded specimens.—Known only from holotype.
Distribution.—Mexico: Distrito Federal. Biome: Chihuahuan Desert.

Eremobates hystrix (Mello-Leitão 1942)

Eremoperna hystrix Mello-Leitão 1942:307.
Eremobates hystrix (Mello-Leitão): Muma 1970:28.

Type material.—Male holotype from Distrito Federal, Mexico (MNRJ).
Recorded specimens.—Known from holotype only.
Distribution.—Mexico: Distrito Federal. Biotic community: Sinaloan Thornscrub.

Eremobates inyoanus
Muma & Brookhart 1988

Eremobates inyoanus Muma & Brookhart 1988:43.

Type material.—Female holotype from Saline Valley, Inyo County, California, USA (CAS).
Recorded specimens.—Four females.
Distribution.—USA: California. Biome: Sonoran Desert.

Eremobates kastoni
Muma & Brookhart 1988

Eremobates kastoni Muma & Brookhart 1988:39.

Type material.—Male holotype and fe-

male allotype from San Diego, California, USA (FSCA).

Recorded specimens.—Several males and females.

Distribution.—USA: California. Biotic community: California Chaparral.

Eremobates kiseri Muma & Brookhart 1988

Eremobates kiseri Muma & Brookhart 1988:15.

Type material.—Male holotype from Turkey, Texas, USA (FSCA). Female allotype from southeast of Turkey, Texas, USA (FSCA).

Recorded specimens.—Several males and females.

Distribution.—USA: Texas. Biome: Chihuahuan Desert.

Eremobates kraepelini Muma 1951

Eremobates mormonus (Roewer): Muma 1951:67 (misidentification).
Eremobates kraepelini Muma 1970:18.

Type material.—Male holotype from Dry Canyon, southeast of Monterey, California, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Arizona, California, Nevada. Biotic community: California Grasslands.

Eremobates leechi Muma & Brookhart 1988

Eremobates leechi Muma & Brookhart 1988:35.

Type material.—Male holotype from 44.8 km south of Livermore, Santa Clara County, California (CAS).

Recorded specimens.—Known from type only.

Distribution.—USA: Northern California. Biotic community: California Grasslands.

Eremobates marathoni Muma 1951

Eremobates marathoni Muma 1951:63; Muma 1988:13 (description of female).

Type material.—Male holotype from Marathon, Texas, USA (AMNH). Female allotype from 9.6 km south of Nuevo Laredo, Mexico (AMNH).

Recorded specimens.—Several males and females.

Distribution.—USA: Southern Texas.

Mexico: Chihuahua. Biome: Chihuahuan Desert.

Eremobates nanus Muma 1962

Eremobates nanus Muma 1962:4.

Type material.—Male holotype from Riverton, Eldorado County, California, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: northeastern California. Biome: Mojave Desert.

Eremobates nivis Muma & Brookhart 1988

Eremobates nivis Muma & Brookhart 1988:34.

Type material.—Male holotype from Snowline Camp, Eldorado County, California (CAS).

Recorded specimens.—Known from type only.

Distribution.—USA: Northern California. Biome: Mojave Desert.

Eremobates nodularis Muma 1951

Eremobates nodularis Muma 1951:69 (male); Muma 1963:6 (female).
Eremobates hessei (Roewer): Muma 1970:18 (misidentification).

Type material.—Male holotype from Carlsbad, New Mexico, USA (AMNH). Female allotype from Portal, Cochise County, Arizona, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: southwestern Texas, southern Arizona, southern California and New Mexico. Mexico: Unknown. Biome: Chihuahuan Desert; Interdesert Grassland; Sonoran Desert.

Eremobates norrisi
Muma & Brookhart 1988

Eremobates norrisi Muma & Brookhart 1988:14.

Type material.—Male holotype and female allotype north of Silver City, New Mexico, USA (FSCA).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Southwestern Texas, Southern New Mexico. Biome: Chihuahuan Desert; Interdesert Grassland.

Eremobates otavonae Muma & Brookhart

Eremobates otavonae Muma & Brookhart 1988:29.

Type material.—Male holotype, male paratype and female allotype from Novato, Marin County, California, USA (CAS).
Recorded specimens.—Four males and one female.
Distribution.—USA: Marin and Napa Counties in North central California. Biotic community: California Grassland.

Eremobates pallidus Muma & Brookhart

Eremobates pallidus Muma & Brookhart 1988:25.

Type material.—Male holotype near Pear Blossom, San Bernadino County, California, USA (AMNH). Female allotype from Deep Canyon, Riverside County, California (UCR).
Recorded specimens.—Numerous males and females.
Distribution.—USA: California, Nevada, Utah. Biome: Sonoran Desert; Mojave Desert.

Eremobates palpisetulosus Fichter 1941

Eremobates palpisetulosus Fichter 1941:179; Muma 1951:61.

Type material.—Male cotypes (syntypes) from Sidney, Nebraska, USA and Harrisburg, Nebraska, USA (AMNH).
Recorded specimens.—Numerous males and females.
Distribution.—USA: Nebraska, Colorado, Kansas, Oklahoma, New Mexico, Northern Texas. Biome: High Dry Grassland.

Eremobates papillatus Muma 1970

Eremobates tuberculatus (Kraepelin): Muma 1951: 72 (misidentification).
Eremobates papillatus Muma 1970:20.

Type material.—Male holotype from Mount Palomar State Park, San Diego County, California, USA (AMNH).
Recorded specimens.—One male and three females.
Distribution.—USA: San Diego County. Mexico: Baja California Norte. Biome: Sonoran Desert; California Sagebrush.

Eremobates pimanus
Muma & Brookhart 1988

Eremobates pimanus Muma & Brookhart 1988:23.

Type material.—Male holotype from Or-gan Pipe Cactus National Monument, Pima County, Arizona, USA (AMNH).
Recorded specimens.—Known from type only.
Distribution.—USA: Southwestern Arizona. Biome: Sonoran Desert.

Eremobates polhemusi
Muma & Brookhart 1988

Eremobates polhemusi Muma & Brookhart 1988: 18.

Type material.—Male holotype from Mesa, Grand Flat, near Hall's Crossing, San Juan County, Utah, USA (AMNH).
Recorded specimens.—Three males, three females collected 4 miles north of Bluff, San Juan County, Utah, USA (DMNH).
Distribution.—USA: Extreme Southeastern Utah. Biome: Interdesert Grassland.

Eremobates purpusi (Roewer 1934)

Eremopus purpusi Roewer 1934:561.
Eremobates purpusi (Roewer): Muma 1970:21 (misidentification, see *Eremobates scopulatus* Muma & Brookhart).

Type material.—Female holotype from Tlaquiloxepec, Mexico, No. 8332 (ZMHU).
Recorded specimens.—Numerous collections of both sexes.
Distribution.—USA, California, Nevada, New Mexico, Utah. Mexico: Coahuila. Biome: Chihuahuan Desert; Mojave Desert; Sonoran Desert; Interdesert Grassland.

Eremobates pyriflora
Muma & Brookhart 1988

Eremobates pyriflora Muma & Brookhart 1988:27.

Type material.—Male holotype from Pear Blossom, San Bernardino County, California, USA (FSCA).
Recorded specimens.—Known from type only.
Distribution.—USA: San Bernadino County, California. Biome: Sonoran Desert.

Eremobates scopulatellus
Muma & Brookhart 1988

Eremobates scopulatellus Muma & Brookhart 1988:40.

Type material.—Male holotype and female allotype from Winchester, Riverside County, California, USA (FSCA).

Recorded specimens.—Numerous males and females.

Distribution.—USA: South central California. Biome: Sonoran Desert.

Eremobates scopulatus Muma 1951

Eremobates scopulatus Muma 1951:67.
Eremobates purpusi (Roewer): Muma 1951:70 (misidentification).

Type material.—Male holotype from Las Vegas, New Mexico, USA (probably Las Vegas, Nevada since all other records are from Utah, Nevada and California). Female allotype from Las Vegas, Nevada, USA (AMNH).

Recorded specimens.—Several males and females.

Distribution.—USA: Nevada, California, Utah. Biome: Mojave Desert.

Eremobates spissus Muma & Brookhart 1988

Eremobates spissus Muma & Brookhart 1988:37.

Type material.—Male holotype from Frank Raines County Park, Stanislaus County, California, USA (CAS). Female allotype and 1 female paratype from west of Westley, Stanislaus County, California, USA (FSCA).

Recorded specimens.—Three males and two females.

Distribution.—USA: California. Biotic community: California Chaparral.

Eremobates tejonus Chamberlin 1925

Eremobates tejonus Chamberlin 1925:236, Muma 1951:70.

Type material.—Male holotype from stomach of *Bufo* sp. from Ft. Tejon, California, USA (MCZ).

Recorded specimens.—Known from type only.

Distribution.—USA: Central California. Biotic community: California Chapparal.

Eremobates texanus Muma & Brookhart 1988

Eremobates texanus Muma & Brookhart 1988:16.

Type material.—Male holotype and female allotype from east of Van Horn, Texas, USA (FSCA).

Recorded specimens.—Six males and six females.

Distribution.—USA: Texas. Biome: Chihuahuan Desert.

Eremobates titschacki (Roewer 1934)

Eremoseta titschacki Roewer 1934:569.
Eremobates affinis (Kraepelin): Muma 1951:65 (misidentification).
Eremobates titschacki (Roewer): Muma 1970:21 (male).

Type material.—Male holotype from California, USA without specific locality (ZSM, Roewer No. 8485).

Recorded specimens.—Several males and females.

Distribution.—USA: Central to northern California. Biotic community: California Steppe.

Eremobates tuberculatus (Kraepelin 1899)

Datames tuberculatus Kraepelin 1899:241 (male).
Eremobates tuberculatus (Kraepelin): Kraepelin 1901:122 (not *Eremobates tuberculatus* (Kraepelin) *sensu* Muma 1951:72).
Eremognatha tuberculata (Kraepelin): Roewer 1934:567 (male).
Eremobates tuberculatus (Kraepelin): Muma 1970: 21 (male).

Type material.—Male holotype from California, USA (ZSM No. 2839, Roewer No. 8374).

Recorded specimens.—Known from type only.

Distribution.—USA: California. Biome: Unknown (lack of type locality).

Eremobates vicinus Muma 1963

Eremobates vicinus Muma 1963:3.

Type material.—Male holotype from Mercury, Nye County, Nevada, USA (AMNH).

Recorded specimens.—Several males and females.

Distribution.—USA: Nevada and California. Biome: Mojave Desert.

Eremobates villosus Muma 1951

Eremobates purpusi (Roewer): Muma 1951:70 (misidentification).
Eremobates villosus Muma 1970: 21.

Type material.—Male holotype and female allotype from Point McCloud Campground, Shasta Lake, Shasta County, California, USA (AMNH).

Recorded specimens.—Several males and females.

Distribution.—USA: California. Biotic community: California Steppe.

Eremobates williamsi
Muma & Brookhart 1988

Eremobates williamsi Muma & Brookhart 1988:33.

Type material.—Male holotype and female allotype from Wildcat Canyon, San Diego County, California, USA (CAS). Male paratype from San Diego area, San Diego County, California, USA (CAS).

Recorded specimens.—Three males and two females.

Distribution.—USA: Southern California. Biotic community: California Sagebrush.

Eremobates scaber group

Eremobates actenidia Muma 1989

Eremobates actenidia Muma 1989:9.

Type material.—Male holotype from Gouldings Trading Post, Monument Valley, San Juan County, Utah, USA (FSCA).

Recorded specimens.—Four males and four females (DMNH).

Distribution.—USA: San Juan County, Utah. Biome: Great Basin Desert.

Eremobates clarus Muma 1989

Eremobates clarus Muma 1989:10.

Type material.—Male holotype from Saratoga Stratton Exp. Watershed, Carbon County, Wyoming, USA (FSCA).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Southwestern Wyoming, Northwestern Colorado. Biome: Cold High Grassland.

Eremobates corpink
Brookhart & Cushing 2004

Eremobates corpink Brookhart & Cushing 2004: 306.

Type material.—Male holotype and female allotype from Coral Pink Sand Dunes, Kane County, Utah, USA (DMNH).

Recorded specimens.—Three males and two females.

Distribution.—USA: Southern Utah. Biome: Great Basin Desert.

Eremobates ctenidiellus Muma 1951

Eremobates ctenidiellus Muma 1951:57.

Type material.—Male holotype and female allotype from Glenwood, Sevier County, Utah, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Colorado and Utah. Biome: Great Basin Desert.

Eremobates hodai Muma 1989

Eremobates hodai Muma 1989:13.

Type material.—Male holotype, with type locality unknown (probably Idaho, USA) (FSCA).

Recorded specimens.—Several males and females.

Distribution.—USA: Snake River Valley, Idaho. Biome: Cold Dry Grassland.

Eremobates icenogelei
Brookhart & Cushing 2004

Eremobates icenogelei Brookhart & Cushing 2004: 300.

Type material.—Male holotype, female allotype, and 5 male and 5 female paratypes from Winchester, San Bernadino County, California, USA (DMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Southeastern California. Biome: Sonoran Desert.

Eremobates legalis Harvey 2002

Datames geniculatus (C.L. Koch): Simon 1879: 138–139, fig. 31 (misidentification).
"*Eremocosta geniculata* (Simon)": Roewer 1934: 570, fig. 324 (misidentification).
"*Eremobates geniculatus* (Simon)": Muma 1970: 10–11; Muma 1987:20 (misidentifications).
Eremobates legalis Harvey 2002:451.
Not "*Eremobates geniculatus* (Simon)": Muma 55, figs. 54–57 (misidentification, see *Eremobates mormonus* (Roewer).

Type material.—Female holotype without precise locality from Mexico (MNHN 2129, Roewer No. 9135.

Recorded specimens.—Known from type only.

Distribution.—Mexico. Biome: Unknown.

Eremobates mormonus (Roewer 1934)

Eremoperna mormona Roewer 1934:561.
Eremobates geniculatus (Simon): sensu Muma 1951:55.
Eremobates mimbrenus Muma 1989:12.
Eremobates mormonus (Roewer): Muma 1963:1.

Type material.—*Eremoperna mormona*: Female holotype from Utah, USA (SMF, No. RII/3466). *Eremobates mimbrenus*: Male and female syntypes from Grant County, New Mexico, USA (FSCA).
Recorded specimens.—Several males and females.
Distribution.—USA: Utah, Arizona. Biome: Interdesert Grassland.

Eremobates scaber (Kraepelin 1899)

Datames scaber Kraepelin 1899:243.
Eremobates scaber (Kraepelin): Kraepelin 1901:124.
Eremostata scabra (Kraepelin): Roewer 1934:124.
Eremobates septentrionis Muma 1951:52.
Eremobates gladiolus Muma 1951:57.
Eremobates scaber (Kraepelin): Brookhart & Cushing 2004:288.

Type material.—*Datames scaber*: Female holotype from "Washington Territory", USA (MNHN, No. 9137). *Eremobates septentrionis*: Male holotype from East Branch, Salt Lake City, Utah, USA (AMNH). *Eremobates gladiolus*: Male holotype from Maupin, Oregon, USA (AMNH). Female allotype from Starbuck, Washington, USA (AMNH).
Recorded specimens.—Numerous males and females.
Distribution.—USA: Oregon, Washington; Canada: British Columbia. Biome: Cold Dry Grassland.

Eremobates similis Muma 1951

Eremobates similis Muma 1951:60.

Type material.—Male holotype from Elk Ridge, Utah, USA (AMNH).
Recorded specimens.—Numerous males and females.
Distribution.—Rio Grande Valley of Colorado and New Mexico, USA. Biome: Chihuahuan Desert; High Dry Grassland.

Eremobates socal
Brookhart & Cushing 2004

Eremobates socal Brookhart & Cushing 2004:304.

Type material.—Male holotype, female al-

lotype from Mt. Palomour, San Bernadino County, California, USA (AMNH).
Recorded specimens.—Three males and four females.
Distribution.—USA: San Bernadino County, California. Biotic community: California Sagebrush.

Eremobates zinni Muma 1951

Eremobates zinni Muma 1951:558.

Type material.—Male holotype and female allotype from Las Vegas, Nevada, USA (AMNH).
Recorded specimens.—Five males and two females.
Distribution.—USA: California, Nevada, Utah. Biome: Mojave Desert.

Genus *Horribates* Muma 1962

Horribates Muma 1962:7.

Horribates bantai Muma

Horribates bantai Muma 1989:17.

Type material.—Female holotype from Saline Valley-Station 18, Inyo County, California, USA (CAS).
Recorded specimens.—Known from type only.
Distribution.—USA: Southern California. Biotic community: California Sagebrush.

Horribates minimus Muma 1989

Horribates minimus Muma 1989:16.

Type material.—Female holotype from Lytle Creek Canyon, San Bernardino County, California, USA (FSCA).
Recorded specimens.—Known from type only.
Distribution.—USA: Southern California. Biotic community: California Sagebrush.

Horribates spinigerus Muma 1962

Horribates spinigerus Muma 1962:7.

Type material.—Female holotype from Borrego State Park, San Diego, California, USA (AMNH).
Recorded specimens.—Two females.
Distribution.—USA: California, Nevada. Biotic community: California Sagebrush.

Subfamily Therobatinae Muma 1951

Therobatinae Muma 1951:85.

Genus *Chanbria* Muma 1951

Chanbria rectus Muma 1962

Chanbria rectus Muma 1962:30.

Type material.—Male holotype from Barstow, San Bernadino County, California, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: Southern California. Biome: Sonoran Desert.

Chanbria regalis Muma 1951

Chanbria regalis Muma 1951:96.

Type material.—Male holotype and 1 male paratype from Twenty-nine Palms, California, USA Female allotype from Palm Springs, California, USA (AMNH).

Recorded specimens.—Several males and females.

Distribution.—USA: Southern California. Biome: Sonoran Desert; Sand Dunes.

Chanbria serpentinus Muma 1951

Chanbria serpentinus Muma 1951:98.

Type material.—Male holotype from Tucson, Arizona, USA (AMNH).

Recorded specimens.—Four males.

Distribution.—USA: Arizona. Biome: Sonoran Desert; Sand Dunes.

Chanbria tehachapianus Muma 1962

Chanbria tehachapianus Muma 1962:29.

Type material.—Male holotype from Tehachapi Mountains, Kern County, California, USA (AMNH).

Recorded specimens.—Known from holotype only.

Distribution.—USA: California. Biotic community: California Steppe; Sand Dunes.

Genus *Eremochelis* Roewer 1934

Eremochelis Roewer 1934:570.
Therobates Muma 1951:85 (synonymized by Muma 1970:30).

Eremochelis andreasana group

Eremochelis andreasana (Muma 1962)

Therobates andreasana Muma 1962:18.
Eremochelis andreasana (Muma): Muma 1970:35.

Type material.—Male holotype and female allotype from Andreas Canyon, Riverside, California, USA (AMNH).

Recorded specimens.—Numerous specimens of both sexes.

Distribution.—USA: California. Mexico: Baja California Norte. Biotic community: California Sagebrush, Sonoran Desert.

Eremochelis sonorae Muma 1987

Eremochelis sonorae Muma 1987:13.

Type material.—Male holotype and female allotype from San Carlos Bay, Sonora, Mexico (CAS).

Recorded specimens.—Known from types only.

Distribution.—Mexico: Sonora. Biome: Sonoran Desert.

Eremochelis branchi group

Eremochelis bechteli Muma 1988

Eremochelis bechteli Muma 1988:23.

Type material.—Male holotype from Whiskey Flat, Mineral County, Nevada, USA (FSCA).

Recorded specimens.—Known from type only.

Distribution.—USA: Nevada. Biome: Great Basin Desert.

Eremochelis bidepressus (Muma 1951)

Hemerotrecha bidepressa Muma 1951:105.
Therobates arcellus Muma 1962:13 (male, not female).
Therobates bidepressus (Muma): Muma 1963:6.
Eremochelis bidepressus (Muma): Muma 1970:30.

Type material.—*Hemerotrecha bidepressa*: Female holotype and 1 female paratype from Reno, Nevada, USA (AMNH). Male allotype from Mercury, Nevada, USA (AMNH). *Therobates arcellus*: Male holotype, female allotype and 1 female paratype from Mercury, Nevada, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Nevada, Idaho, Washington, Utah. Biome: Mojave Desert; Great Basin Desert.

Eremochelis branchi (Muma 1951)

Therobates branchi Muma 1951:85.
Eremochelis branchi (Muma): Muma 1970:20.

Type material.—Male holotype from

Twenty-nine Palms, California, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Southern California, Arizona, Nevada. Biome: Sonoran Desert; Mojave Desert; Great Basin Desert.

Eremochelis coloradensis (Muma 1962)

Therobates coloradensis Muma 1962:9.
Eremochelis coloradensis (Muma): Muma 1970:31.

Type material.—Female holotype from Grand Canyon, Arizona, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: Arizona. Biome: Interdesert Grassland.

Eremochelis flavus Muma 1989

Eremochelis flavus Muma 1989:85.

Type material.—Female holotype from Winterhaven, California, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: Southern California. Biome: Sonoran Desert

Eremochelis fuscellus Muma 1989

Eremochelis fuscellus Muma 1989:22.

Type material.—Male holotype, female allotype and 1 male paratype from Newberry, San Bernadino County, California, USA (FSCA).

Recorded specimens.—Known from types only.

Distribution.—USA: Southern California. Biome: Sonoran Desert.

Eremochelis gertschi (Muma 1951)

Therobates gertschi Muma 1951:86.
Eremochelis gertschi (Muma): Muma 1970:31.

Type material.—Female holotype from Zion National Park, Utah, USA (AMNH).

Recorded specimens.—Six males and females.

Distribution.—USA: Utah. Biome: Great Basin Desert.

Eremochelis insignatus Roewer 1934

Eremochelis insignatus Roewer 1934:570.
Therobates cameronensis Muma 1951:90 (synonymized by Muma 1970:31).

Hemerotrecha insignita (Roewer): Muma 1951:108.
Therobates arcellus Muma 1962:13 (misidentification, females only).
Eremochelis arcellus (Muma): Muma 1976:18.
Eremochelis cameronensis (Muma): Muma 1976:19.
Eremochelis insignatus Roewer: Muma 1970:31.

Type material.—*Eremochelis insignatus*: Male holotype from California, USA (SMF, No. 3014). Female "allotype" from Mercury, Nevada (AMNH). *Therobates cameronensis*: Male holotype from Cameron, Arizona, USA (AMNH). *Therobates arcellus*: Male holotype, female allotype, and 2 female paratypes from Mercury, Nevada, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Arizona, California, Colorado, Nevada. Biome: Great Basin Desert; Mojave Desert.

Eremochelis iviei (Muma 1951)

Therobates iviei Muma 1951:88.
Eremochelis iviei (Muma): Muma 1970:32.

Type material.—Female holotype from Colossal Cave Camp, Pima County, Arizona, USA (AMNH). Male allotype from Colossal Cave, Pima County Arizona, USA (FSCA).

Recorded specimens.—Known from types only.

Distribution.—USA: Arizona. Biome: Sonoran Desert.

Eremochelis malkini (Muma 1951)

Therobates malkini Muma 1951:88.
Eremochelis malkini (Muma): Muma 1970:34.

Type material.—Female holotype from southern rim of Grand Canyon, Arizona, USA (AMNH).

Recorded specimens.—Three females.

Distribution.—USA: Arizona. Biome: Interdesert Grassland.

Eremochelis medialis (Muma 1951)

Therobates medialis Muma 1951:90.
Eremochelis medialis (Muma): Muma 1970:32.

Type material.—Male holotype from California, USA (originally deposited at University of Utah but now at AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: California. Biome: Sonoran Desert.

Eremochelis oregonensis
Brookhart & Cushing 2002

Eremochelis oregonensis Brookhart & Cushing 2002:95.

Type material.—Male holotype from Valley Falls, Lake County, Oregon, USA (DMNH).
Recorded specimens.—Known from type only.
Distribution.—USA: Oregon. Biome: Great Basin Desert.

Eremochelis saltoni Muma 1989

Eremochelis saltoni Muma 1989:24.

Type material.—Female holotype from 16 km south of Salton City, California, USA (FSCA).
Recorded specimens.—Numerous males and females.
Distribution.—USA: Southern California. Biome: Sonoran Desert.

Eremochelis tanneri Muma 1989

Eremochelis tanneri Muma 1989:24.

Type material.—Female holotype from the Tecoma Range, Copper Mts., near Lucin, Box Elder County, Utah, USA (FSCA).
Recorded specimens.—Known from type only.
Distribution.—USA: Utah. Biome: Great Basin Desert.

Eremochelis bilobatus group

Eremochelis acrilobatus (Muma 1962)

Therobates acrilobatus Muma 1962:10.
Eremochelis acrilobatus (Muma): Muma 1970:32.

Type material.—Female holotype from Quail Springs, Joshua Tree National Monument, California, USA (AMNH).
Recorded specimens.—Known from type only.
Distribution.—USA: Southern California. Biome: Sonoran Desert.

Eremochelis arcus (Muma 1962)

Therobates arcus Muma 1962:11.
Eremochelis arcus (Muma): Muma 1970:33.

Type material.—Male holotype and female allotype from Taft, California, USA (AMNH).
Recorded specimens.—Two males and one female.
Distribution.—USA: California and Nevada. Biome: Sonoran Desert; Biotic community: California steppe.

Eremochelis bilobatus (Muma 1951)

Datames pallipes Say: Simon 1879:139 (misidentification, in part).
Eremobates pallipes (Say): Banks 1900:427; Kraepelin 1901:126 (misidentifications); Roewer 1934:555.
Therobates bilobatus Muma 1951:92.
Eremochelis bilobatus (Muma): Muma 1970:33.

Type material.—Male holotype from Davis Mountains, Texas, USA (AMNH). Female allotype from Chiricahua Mountains, Arizona, USA (AMNH).
Recorded specimens.—Numerous males and females.
Distribution.—USA: Arizona, California, Colorado, New Mexico, Texas. Biome: Sonoran Desert; Chihuahuan Desert; Interdesert Grassland; High Dry Grassland; Cold Dry Grassland.

Eremochelis cochiseae Muma 1989

Eremochelis cochiseae Muma 1989:32.

Type material.—Male holotype, female allotype, 6 male and 3 female paratypes from Portal, Cochise County, Arizona, USA (FSCA).
Recorded specimens.—Seven males and four females.
Distribution.—USA: Arizona. Biome: Sonoran Desert.

Eremochelis cuyamacanus (Muma 1962)

Therobates cuyamacanus Muma 1962:17.
Eremochelis cuyamacanus (Muma): Muma 1970:34.

Type material.—Male holotype and 1 male paratype from Cuyamaca, California, USA (AMNH).
Recorded specimens.—Known from types only.
Distribution.—USA: California. Biome: Sonoran Desert.

Eremochelis flexacus (Muma 1963)

Therobates flexacus Muma 1963:3.
Eremochelis flexacus (Muma): Muma 1970:34.

Type material.—Male holotype and 2 male paratypes from Mercury, Nevada, USA (AMNH).

Recorded specimens.—Three males and one female.

Distribution.—USA: Nevada. Mexico, Baja Callifornia. Biome: Mojave Desert.

Eremochelis giboi Muma 1989

Eremochelis giboi Muma 1989:28

Type material.—Male holotype from northeast El Paso Mts., Kern County, California, USA (FSCA).

Recorded specimens.—Known from type only.

Distribution.—USA: California. Biome: California Steppe.

Eremochelis kerni Muma 1989

Eremochelis kerni Muma 1989:30.

Type material.—Male holotype from Roads End, Kern River, Tulare County, California, USA (FSCA). Female allotype from Pearblossom, San Bernardino County, California, USA (FSCA).

Recorded specimens.—Known from types only.

Distribution.—USA: California. Biotic community: California Steppe.

Eremochelis lagunensis Vázquez 1991

Eremochelis lagunensis Vázquez 1991:88.

Type material.—Male holotype, female allotype and 2 male paratypes from Valle de La Laguna, Baja California Sur, Mexico (in collection of I. Vázquez).

Recorded specimens.—Known from types only.

Distribution.—Mexico: Baja California Sur. Biome: Sonoran Desert.

Eremochelis macswaini (Muma 1962)

Therobates macswaini Muma 1962:17.
Eremochelis macswaini (Muma): Muma 1970:34.

Type material.—Male holotype from Crystal Lake, Los Angeles County, California, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: California. Biome: Sonoran Desert.

Eremochelis morrisi (Muma 1951)

Therobates morrisi Muma 1951:90.
Eremochelis morrisi (Muma): Muma 1970:32.

Type material.—Male holotype from Los Angeles, California, USA (AMNH). Female allotype from Riverside County, California, USA (FSCA).

Recorded specimens.—Several males, one female.

Distribution.—USA: Southern California. Biotic community: California Sagebrush.

Eremochelis noonani Muma 1989

Eremochelis noonani Muma 1989:29.

Type material.—Male holotype from Miller Canyon, Eldorado County, California, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: California. Biome: Sonoran Desert.

Eremochelis nudus Muma 1963

Therobates nudus Muma 1963:4.
Eremochelis nudus (Muma): Muma 1970:35.

Type material.—Male holotype from Mercury, Nevada, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: Nevada. Biome: Mojave Desert.

Eremochelis plicatus (Muma 1962)

Therobates plicatus Muma 1962:11.
Eremochelis plicatus (Muma): Muma 1970:33.

Type material.—Male holotype, female allotype and unspecified number of paratypes from Mercury, Nevada, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Nevada. Biome: Mojave Desert.

Eremochelis rossi Muma 1987

Eremochelis rossi Muma 1987:11.

Type material.—Male holotype from 3.3 km elevation on north slope of Mt. Popocatepetl, Mexico (CAS).

Recorded specimens.—Known from type only.

Distribution.—Mexico: Desitiro Federal. Biotic community: Sinaloan Thornshrub.

Eremochelis truncus Muma 1987

Eremochelis truncus Muma 1987:11.

Type material.—Female holotype from Isla Coyote, just north of Isla San Francisco, Baja California Sur, Mexico (CAS).

Recorded specimens.—Known from type only.

Distribution.—Mexico. Biome: Sonoran Desert.

Eremochelis imperalis group

Eremochelis imperialis (Muma 1951)

Therobates imperialis Muma 1951:94.
Therobates attritus Muma 1963:4.
Eremochelis attritus (Muma): Muma 1976:20.
Eremochelis imperialis (Muma): Muma 1970:35.

Type material.—*Therobates imperialis*: Male holotype from Palo Verde, Imperial County California, USA (AMNH). Female allotype and 1 paratype from Nye County, Nevada, USA (AMNH). *Therobates attritus*: Female holotype from Mercury, Nevada, USA (FSCA).

Recorded specimens.—Three males and two females.

Distribution.—USA: Arizona, California, Nevada. Mexico: Sonora. Biome: Sonoran Desert.

Eremochelis kastoni Rowland 1974

Eremochelis kastoni Rowland 1974:1.

Type material.—Male holotype, female allotype, and 8 male and 6 female paratypes from San Diego, San Diego County, California, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: California. Biotic community: California Sagebrush.

Eremochelis larreae (Muma 1962)

Therobates larreae Muma 1962:21.
Eremochelis larreae (Muma): Muma 1970:35.

Type material.—Male holotype and female allotype from Mule Canyon, Calico Mountains, San Bernadino County, California, USA (AMNH).

Recorded specimens.—Four males and one female.

Distribution.—USA: California. Biome: Sonoran Desert.

Eremochelis rothi (Muma 1962)

Therobates rothi Muma 1962:24.
Eremochelis rothi (Muma): Muma 1970:36.

Type material.—Male holotype from Welton, Yuma County, Arizona, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: Arizona. Biome: Sonoran Desert.

Eremochelis undulus Muma 1989

Eremochelis undulus Muma 1989:34.

Type material.—Male holotype from pits along Sidewinder Road, 17 km west of Colorado River, California, USA (FSCA).

Recorded specimens.—Known from type only.

Distribution.—USA: California. Biome: Sonoran Desert.

Eremochelis striodorsalis group

Eremochelis striodorsalis (Muma 1962)

Therobates striodorsalis Muma 1962:25.
Eremochelis striodorsalis (Muma): Muma 1970:36.

Type material.—Male holotype from Pine Valley, San Diego County, California, USA (AMNH).

Recorded specimens.—Two males.

Distribution.—USA: California. Biotic community: California Sagebrush.

Genus *Hemerotrecha* Banks 1903

Hemerotrecha Banks 1903:78.
Eremochelis Roewer 1934:570 (in part).
Eremognatha Roewer 1934:566 (in part).

Hemerotrecha banksi group

Hemerotrecha banksi Muma 1951

Hemerotrecha californica Banks 1903:79 (junior secondary homonym of *Cleobis californica* Banks, 1899).
Hemerotrecha banksi Muma 1951:99 (replacement name).

Type material.—Male holotype from Pacific Grove, California, USA (MCZ).

Recorded specimens.—Numerous males and females.

Distribution.—USA: California. Biotic community: California Chaparral.

Hemerotrecha californica (Banks 1899)

Cleobis californica Banks 1899:314.
Ammotrecha californica (Banks): Banks 1900:427.
Hemerotrecha californica (Banks): Banks 1904: 363.

Type material.—Female holotype from Los Angeles, California, USA (MCZ).

Recorded specimens.—Numerous males and females.

Distribution.—USA: California, Idaho, Nevada, Oregon and Washington. Biome: Sonoran Desert; Mojave Desert; Great Basin Desert; Biotic community: California Chaparral; California Grassland.

Hemerotrecha marginata (Kraepelin 1911)

Eremobates marginatus Kraepelin 1911:103.
Eremognatha marginata (Kraepelin): Roewer 1934: 567.
Hemerotrecha marginata (Kraepelin): Muma 1951: 102.

Type material.—Male holotype and female allotype from San Pedro, California, USA (ZSM Roewer No. 8376).

Recorded specimens.—Several males and females.

Distribution.—USA: California. Biotic community: California Chaparral.

Hemerotrecha truncata Muma 1951

Hemerotrecha truncata Muma 1951:102.

Type material.—Male holotype from Exeter, Tulare County, California, USA (AMNH).

Recorded specimens.—Five males and two females.

Distribution.—USA: California. Biotic community: California Steppe.

Hemerotrecha branchi group

Hemerotrecha bixleri Muma 1989

Hemerotrecha bixleri Muma 1989:44.

Type material.—Male holotype, 1 male paratype and female allotype from Tucson Mts., Arizona, USA (FSCA).

Recorded specimens.—Known from types only.

Distribution.—USA: Arizona. Biome: Sonoran Desert.

Hemerotrecha branchi Muma 1951

Hemerotrecha branchi Muma 1951:112.

Type material.—Male holotype from Twenty-nine Palms, California, USA (AMNH).

Recorded specimens.—Five males.

Distribution.—USA: Arizona, California, Nevada and New Mexico. Biome: Sonoran Desert, Interdesert Grassland.

Hemerotrecha cornuta Brookhart & Cushing 2002

Hemerotrecha cornuta Brookhart & Cushing 2002: 91.

Type material.—Male holotype, female allotype and 5 male and 2 female paratypes from Boone, Colorado, USA (DMNH).

Recorded specimens.—Known from types only.

Distribution.—USA: Eastern Colorado. Biome: High Dry Grassland.

Hemerotrecha cazieri Muma 1986

Hemerotrecha cazieri Muma 1986:13.

Type material.—Male holotype from sand dunes, San Luis, Sonora, Mexico (CAS).

Recorded specimens.—Known from type only.

Distribution.—Mexico: Sonora. Biome: Sonoran Desert.

Hemerotrecha macra Muma 1951

Hemerotrecha macra Muma 1951:114.

Type material.—Male holotype from Lugert, Oklahoma, USA (originally at University of Utah but now at AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: Oklahoma. Biome: High Dry Grassland.

Hemerotrecha milsteadi Muma 1962

Hemerotrecha milsteadi Muma 1962:35.

Type material.—Female holotype from Sierra Vieja, Valentine, Presidio County, Texas, USA (AMNH). Male allotype from Van Horn, Texas, USA (FSCA).

Recorded specimens.—Known from types only.

Distribution.—USA: New Mexico and Texas. Biome: Chihuahuan Desert.

Hemerotrecha minima Muma 1951

Hemerotrecha minima Muma 1951:114.

Type material.—Male holotype from Laredo, Texas, USA (AMNH).
Recorded specimens.—Two males.
Distribution.—USA: Texas. Biome: Chihuahuan Desert.

Hemerotrecha sevilleta Brookhart & Cushing 2002

Hemerotrecha sevilleta Brookhart & Cushing 2002: 93.

Type material.—Male holotype, female allotype, 4 males and 3 female paratypes from Sevilleta National Wildlife Reserve, Socorro County, New Mexico, USA (DMNH).
Recorded specimens.—Several males and females.
Distribution.—USA: New Mexico. Biome: Chihuahuan Desert.

Hemerotrecha xena Muma 1951

Hemerotrecha xena Muma 1951:112.

Type material.—Male holotype from Coyote Wells, Colorado Desert, California, USA (CUM).
Recorded specimens.—Known from type only.
Distribution.—USA: California. Biome: Sonoran Desert.

Hemerotrecha denticulata group

Hemerotrecha carsonana Muma 1989

Hemerotrecha carsonana Muma 1989:41.

Type material.—Male holotype from Carson City, Lyon County, Nevada, USA (FSCA).
Recorded specimens.—Known from type only.
Distribution.—USA: Nevada. Biome: Mojave Desert.

Hemerotrecha delicatula Muma 1989

Hemerotrecha delicatula Muma 1989:40.

Type material.—Male holotype from Nipple Bench, Kane County, Utah, USA (BYU).
Recorded specimens.—Known from type only.
Distribution.—USA: Utah. Biome: Great Basin Desert.

Hemerotrecha denticulata Muma 1951

Hemerotrecha denticulata Muma 1951:105.

Type material.—Male holotype, female allotype, and 3 male and 3 female paratypes from Reno, Nevada, USA (AMNH).
Recorded specimens.—Several males and females.
Distribution.—USA: California, Colorado, Idaho, Nevada, Utah and Washington. Canada: British Columbia. Biome: Mojave Desert; Great Basin Desert; Cold Dry Grassland.

Hemerotrecha neotena Muma 1989

Hemerotrecha neotena Muma 1989:41.

Type material.—Male holotype, female allotype, and 1 male paratype from Coconino County, Arizona, USA (FSCA).
Recorded specimens.—Known from types only.
Distribution.—USA: Arizona. Biome: Interdesert Grassland.

Hemerotrecha parva Muma 1989

Hemerotrecha parva Muma 1989:39.

Type material.—Male holotype from Vernal, Utah, USA (CAS).
Recorded specimens.—Known from type only.
Distribution.—USA: Utah. Biome: Great Basin Desert.

Hemerotrecha proxima Muma 1963

Hemerotrecha proxima Muma 1963:4.

Type material.—Male holotype, female allotype, 1 male and 1 female paratype from Mercury, Nevada, USA (AMNH).
Recorded specimens.—Three males and two females.
Distribution.—USA: Nevada. Biome: Mojave Desert.

Hemerotrecha serrata group

Hemerotrecha serrata Muma 1951

Hemerotrecha serrata Muma 1951:102.

Type material.—Male holotype from Twenty-nine Palms, California, USA (AMNH).
Recorded specimens.—Numerous males and females.
Distribution.—USA: Southern California

and southern Nevada. Biome: Sonoran Desert; Mojave Desert; Great Basin Desert.

Hemerotrecha simplex group

Hemerotrecha fruitana Muma 1951

Hemerotrecha fruitana Muma 1951:106.

Type material.—Male holotype from Fruita, Utah, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: California, Colorado, Nevada, New Mexico, Utah and Wyoming. Biome: Mojave Desert; Great Basin Desert; High Desert Grassland.

Hemerotrecha jacinotoana Muma 1962

Hemerotrecha jacinotoana Muma 1962:33.

Type material.—Female holotype from Idyllwild, San Jacinto Mountains, California, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: California. Biome: Sonoran Desert.

Hemerotrecha maricopana Muma 1989

Hemerotrecha maricopana Muma 1989:37.

Type material.—Female holotype from South Mountain, Maricopa County, Arizona, USA (CAS).

Recorded specimens.—Known from type only.

Distribution.—USA: Arizona. Biome: Sonoran Desert.

Hemerotrecha nevadensis Muma 1951

Hemerotrecha nevadensis Muma 1951:110.

Type material.—Female holotype from Las Vegas, Nevada, USA (AMNH).

Recorded specimens.—Two females, including holotype.

Distribution.—USA: Nevada. Biome: Mojave Desert.

Hemerotrecha simplex Muma 1951

Hemerotrecha simplex Muma 1951:110.

Type material.—Male holotype from Dry Lake Station, San Diego, California, USA (CUM).

Recorded specimens.—Four males, including holotype.

Distribution.—USA: Arizona, California. Biotic community: California Chaparral.

Hemerotrecha steckleri Muma 1951

Hemerotrecha steckleri Muma 1951:111.

Type material.—Female holotype from Canada del Oro, Santa Catalina Mountains, Arizona, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: Arizona. Biome: Sonoran Desert.

Hemerotrecha werneri Muma 1951

Hemerotrecha werneri Muma 1951:111.

Type material.—Male holotype from Cutler, Gila County, Arizona, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: Arizona. Biome: Sonoran Desert.

Hemerotrecha texana group

Hemerotrecha texana Muma 1951

Hemerotrecha texana Muma 1951:104.

Type material.—Male holotype from Hot Springs, Texas, USA (AMNH).

Recorded specimens.—Known from type only.

Distribution.—USA: Texas. Biome: Chihuahuan Desert.

Family AMMOTRECHIDAE Roewer 1934

Ammotrechidae Roewer 1934:578.

Key to males of North American Family Ammotrechidae (males only)
(Modified from Muma (1970))

1. Tarsi of fourth leg with 3 segments 2
   Tarsi of fourth leg with 1 segment . . . . *Branchia*
2. Distal segment of tarsi IV with one pair of ventral spine-like setae . . . . *Ammotrechella*
   Distal segment of tarsi IV with more then one pair of ventral spine-like setae 3

3. Tarsi IV with 2,2–2–2,2 (see Muma 1951) formula of ventral spine-like setae   *Ammotrechula*
   Tarsi IV with 2,2–2–2,1 formula of ventral spine-like setae . . . .   *Ammotrecha*

Subfamily AMMOTRECHINAE Roewer

Ammotrechinae Roewer 1934:590; Muma 1951:
   123.

Ammotrecha Banks 1900

Cleobis Simon 1879:145 (junior homonym).
Ammotrecha Banks 1900:426.

Ammotrecha chiapasi Muma 1986

Ammotrecha chiapasi Muma 1986:15.

Type material.—Male holotype, female al-
lotype, 2 male paratypes and 1 female para-
type taken in house, San Cristobal de las Ca-
sas, Chiapas, Mexico (CAS).
Recorded specimens.—Known from types
only.
Distribution.—Mexico: Chiapas. Biotic
community: Sinaloan thornscrub.

Ammotrecha cobinensis Muma 1951

Ammotrecha cobinensis Muma 1951:135.

Type material.—Male holotype from Co-
bina, California, USA (originally deposited at
University of Utah but now at AMNH).
Recorded specimens.—Two males.
Distribution.—USA: California. Mexico:
Unknown (Muma 1970, 1986). Biome: So-
noran Desert.

Ammotrecha itzaana Muma 1987

Ammotrecha itzaana Muma 1987:16.

Type material.—Male holotype and male
paratype from Chechen Itza, Yucatan, Mexico
(AMNH).
Recorded specimens.—Known from types
only.
Distribution.—Mexico: Yucatan. Biome:
Savannah.

Ammotrecha limbata (Lucas 1835)

Galeodes limbata Lucas 1835: Cl. 8.
Ammotrecha limbata (Lucas): Kraepelin 1901:112;
   Roewer 1934:597.

Type material.—Location of the type
(*Galeodes limbata*) unknown and a lectotype
from Guatemala, number 8356 in ZSM cannot
be located.
Recorded specimens.—Three males and
two females.

Distribution.—Central America: Guate-
mala. North America: Mexico. Biome: Un-
known.

Ammotrecha stolli (Pocock 1895)

Cleobis stolli Pocock 1895:97.
Ammotrecha stolli (Pocock): Kraepelin 1901:115.
Ammotrecha picta Pocock 1902:65; Roewer 1934:
   597.

Type material.—*Cleobis stolli*: Female ho-
lotype from Retalhuleau, Guatemala (BMNH,
Roewer No. 8605). *Ammotrecha picta*: Gua-
temala. The types of *A. picta* have not been
located.
Recorded specimens.—Four males of *A.
stolli*, several females.
Distribution.—Central America: Guate-
mala, Costa Rica, Grenada, Nicaragua. USA:
Louisiana. Mexico: Chiapas, Guerrereo, Mi-
choacan. Biome: Sinoloan Thornscrub, possi-
bly beach sand.

Genus *Ammotrechella* Roewer 1934

Ammotrecha Banks 1900:426 (in part).
Ammotrechella Roewer 1934:594; Muma 1951:125.

Ammotrechella bolivari Mello-Leitão 1942

Ammotrechella bolivari Mello-Leitão 1942:309.

Type material.—Female holotype from
Chiapas, Mexico (MNRJ).
Recorded specimens.—Known from type
only.
Distribution.—Mexico: Chiapas. Biotic
community: Sinaloan Thornshrub.

Ammotrechella pseustes (Chamberlin 1925)

Ammotrecha pseustes Chamberlin 1925:235.
Ammotrechella sexpicata Muma 1951:129.
Ammotrechella pseustes (Chamberlin): Muma
   1970:47.

Type material.—*Ammotrecha pseustes*:
Female holotype from Isla Largo Remo, Canal
Zone, Panama (MCZ). *Ammotrechella sexpi-
cata*: Female holotype from Claremont, Cali-
fornia, USA (originally at University of Utah,
now at AMNH).
Recorded specimens.—Known from types
only.
Distribution.—Central   America: Canal

Zone, Panama, West Indies: Puerto Rico (females only). USA: California. Mexico. Biome: Unknown, possibly beach sand.

Ammotrechella setulosa Muma 1951

Ammotrechella setulosa Muma 1951:125.

Type material.—Female holotype from Eagle Pass, Texas, USA (USNM).
Recorded specimens.—Known from type only.
Distribution.—USA: Texas. Biome: Chihuahuan Desert.

Ammotrechella stimpsoni (Putnam 1882)

Galeodes (*Cleobis*) *stimpsoni* Putnam 1882:261.
Ammotrecha cubae (Lucas): Banks 1900:427 (misidentification).
Ammotrechella stimpsoni (Putnam): Muma 1951: 127.

Type material.—Type at MCZ apparently lost or destroyed.
Recorded specimens.—Numerous males and females.
Distribution.—USA: Florida. Biotic community: Widely distributed in sandy soil. Muma (pers. comm.) collected them in mangrove stems.

Genus *Ammotrechula* Roewer 1934

Ammotrechula Roewer, 1934:600

Ammotrechula boneti Mello-Leitão 1942

Ammotrechula boneti Mello-Leitão 1942:312.

Type material.—Male holotype from Mazatlan, Mexico (MNRJ).
Recorded specimens.—Known from type only.
Distribution.—Mexico: Sinoloa. Biome: Sonoran Desert.

Ammotrechula borregoensis Muma 1962

Ammotrechula borregoensis Muma 1962:41; Muma 1989:48
Ammotrechula dolabra Muma 1963:5.

Type material.—*Ammotrechula borregoensis*: Female holotype from Borrego State Park, San Diego, California, USA (AMNH). *Ammotrechula dolabra*: Male holotype from Cane Springs, Nevada, USA (AMNH).
Recorded specimens.—Known from two males and one female.
Distribution.—USA: California, Nevada. Biome: Sonoran Desert.

Ammotrechula catalinae Muma 1988

Ammotrechula catalinae Muma 1988:47.

Type material.—Female holotype and 2 immatures from Santa Catalina Mountains, Pima County, Arizona, USA (FSCA).
Recorded specimens.—Several males and females.
Distribution.—USA: California. Biome: Sonoran Desert.

Ammotrechula lacuna Muma 1963

Ammotrechula lacuna Muma 1963:5.

Type material.—Male holotype from Mercury, Nevada, USA (AMNH).
Recorded specimens.—Known from one male and one female.
Distribution.—USA: Nevada. Biome: Mojave Desert.

Ammotrechula mulaiki Muma 1951

Ammotrechula mulaiki Muma 1951:130.

Type material.—Male holotype from Edinburg, Texas, USA (AMNH).
Recorded specimens.—Known from type only.
Distribution.—USA: Texas. Biome: Chihuahuan Desert.

Ammotrechula peninsulana (Banks 1898)

Cleobis peninsulana Banks 1898:290.
Cleobis hirsuta Banks 1898:291.
Cleobis texana Kraepelin 1899:239.
Ammotrecha texana (Banks): Kraepelin 1901:112.
Ammotrechula texana (Banks): Roewer 1934:601.
Ammotrechula peninsulana (Banks): Muma 1951: 130.

Type material.—*Cleobis peninsulana*: Female holotype from San Jose del Cabo, Baja California, Mexico (MCZ). *Cleobis hirsuta*: Male holotype from San Miguel de Horcasitas, Baja California, Mexico (MCZ). *Cleobis texana*: Female holotype from Texas, USA (MNHN, Roewer No. 9099).
Recorded specimens.—Numerous males and females.
Distribution.—USA: Arizona, New Mexico. Mexico: Baja California Sur, Chihuahua, Sinoloa, Sonora. Biome: Chihuahuan Desert; Sonoran Desert; Interdesert Grassland.

Ammotrechula pilosa Muma 1951

Ammotrechula pilosa Muma 1951:134.

Type material.—Female holotype from Texas, USA (DZUU).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Arizona, California, Nevada and Texas. Biome: Chihuahuan Desert; Sonoran Desert; Mojave Desert.

Ammotrechula saltatrix (Simon 1879)

Cleobis saltatrix Simon 1879:146.
Ammotrecha saltatrix (Simon): Kraepelin 1901: 113.
Ammmotrechula saltatrix (Simon): Roewer 1934: 602.
Ammotrechula saltatrix (Simon): Muma 1970:54.

Type material.—Female holotype from Mexico (MNHN, No. 9098).

Recorded specimens.—One male and two females.

Distribution.—Mexico: Baja California. Biome: Sonoran Desert.

Ammotrechula venusta Muma 1951

Ammotrechula venusta Muma 1951:134.

Type material.—Male holotype from Tucson, Arizona, USA (AMNH).

Recorded specimens.—One male and 1 female.

Distribution.—USA: Arizona. Mexico: Jalisco. Biome: Sonoran Desert.

Ammotrechula wasbaueri Muma 1962

Ammotrechula wasbaueri Muma 1962:43.

Type material.—Male holotype from Andreas Canyon, Riverside County, California, USA (AMNH).

Recorded specimens.—Three males.

Distribution.—USA: California. Biome: California Chaparral.

SUBFAMILY SARONOMINAE ROEWER

Saronominae Roewer 1934:580; Muma 1951:135.

Genus *Branchia* Muma 1951

Branchia Muma 1951:135.

Branchia angustus Muma 1951

Branchia angustus Muma 1951:135.

Type material.—Male holotype and 3 male paratypes from Twenty-nine Palms, California, USA (AMNH).

Recorded specimens.—Four males, two females.

Distribution.—USA: Arizona, California. Mexico: Sonora. Biome: Mojave Desert.

Branchia brevis Muma 1951

Branchia brevis Muma 1951:137.

Type material.—Male holotype from Edinburg, Texas, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: Arizona, Texas, New Mexico. Biome: Chihuahuan Desert; Interdesert Grassland.

Branchia potens Muma 1951

Branchia potens Muma 1951:138.

Type material.—Male holotype from Twenty-nine Palms, California, USA (AMNH).

Recorded specimens.—Numerous males and females.

Distribution.—USA: California, Nevada, Utah. Mexico. Biome: Mojave Desert; Sonoran Desert; Great Basin Desert.

DISCUSSION

With this checklist the North American Eremobatinae has been reduced to five genera including Harvey's (2002, 2003) reconstruction of the genera *Eremorhax* and *Eremocosta*. There has been the addition of 60 new species bringing the number to 104 species (Table 1). The number of Therobatinae genera has been reduced to three as a result of Muma's (1970) synonymy of *Therobates* with *Eremochelis*. The species number is 70, an increase of 21 species (Table 2). The Ammotrechinae have four genera and 22 species, an addition of only three new species over 40 years which is not surprising considering the lack of investigative work and the subtropical distribution of this group (Table 3). Fifty-six species are known from the type only and many from only one sex. Muma (pers. comm.) realized that the classification system used with the ammotrechids was cumbersome and faulty, and Harvey (2003) exhorts someone to begin a complete overhaul of the entire system started by Roewer and refined by Muma (1951).

Table 1.—Number of Eremobatinae solifugid species in continental North America.

Genera	Groups	Number of species
Eremorhax		10
Eremocosta		13
Eremothera		2
Eremobates	Angustus	3
	Aztecus	1
	Lapzi	1
	Pallipes	18
	Palpisetulosus	41
	Scaber	12
Horribates		3
Total 5	6	104

Because most of the data has come as the result of pitfall trapping in a limited number of areas, caution should be used in basing too many conclusions about the abundance and distribution of solifugids. Since solifugids are for the most part nocturnal and rarely collected, their distribution is sketchy and for the most part skewed towards those communities where some long term collections have taken place (Allred & Muma 1971; Muma 1974a, 1974b; Brookhart & Brantley 2000).

It is likely that collection of more specimens from specific type localities will lead to combining one or more of the putative species. The authors have found that a species

Table 2.—Number of Therobatinae solifugid species in continental North America.

Genera	Groups	Number of species
Chanbria		4
Eremohelis	Andreasana	2
	Branchi	14
	Bilobatus	16
	Imperialis	5
	Striodorsalis	1
Hemerotrecha	Banksi	4
	Branchi	9
	Denticulata	6
	Serrata	1
	Simplex	7
	Texana	1
Total 3	11	70

Table 3.—Number of Ammotrechid solifugid species in continental North American.

Genera	Number of species
Ammotrecha	5
Ammotrechella	4
Ammotrechula	10
Branchia	3
Total 4	22

known from only one or two specimens is often valid (Brookhart & Cushing 2002). Readers are referred to Scharff et al. (2003) for the discussion of "singletons".

This is the first specific attempt to organize solifugids in terms of biogeographic distribution. A few generalizations can be made. At the generic and specific levels it should be pointed out that although certain genera and species are found in two or more deserts or grasslands, others are confined to only one desert or grassland. The four major recognized deserts of North America support a large, more diversified solifugid fauna than the adjacent arid grasslands (Table 4). Although each supports a distinctive solifugid fauna, there are some species that are found in several biomes. This may indicate a greater ability to occupy a variety of niches but more likely it indicates that these identified species are really more than one and further investigation is warranted. Recent studies indicate that most species of solifugids occupy a more narrow geographical range than previously

Table 4.—Number of solifugid species recorded in continental North American biomes. (Total number exceeds number of identified species ($n = 192$) because some species are found in more than one biome.)

Biome	Number of species
Chihuahua Desert	32
Sonoran Desert	82
Mojave Desert	28
Great Basin Desert	18
Interdesert Grassland	22
High Dry Grassland	10
Cold Dry Grassland	6
California Xeric Localities	33
Sinoloan Thornshrub	8

thought (Brookhart & Brantley 2000; Brookhart & Cushing 2004). Members of species groups appear to be allopatric, with only the *E. palpisetulosus* group showing much sympatry (Brookhart & Muma 1981, 1987; Muma & Brookhart 1988; Brookhart & Cushing 2004).

The Sonoran Desert supports the greater number of genera (11) and species (82) despite the fact that it is the hottest and driest and has been subject to the least long term investigation. The Chihuahuan has only 8 genera and 32 species even though it has been the subject of most of the long term studies used in this paper. As expected, the cold deserts have the fewest solifugids. The Mohave Desert is inhabited by 4 genera, 28 species and Great Basin Desert has 7 genera and 18 species (Table 4). Seven genera and 63 species are found in Mexico and two genera and three described and one undescribed species are found in Canada.

Five genera (*Chanbria, Horribates, Eremothera, Therobates, Ammotrecha*) have not been collected in great numbers. *Chanbria* has been collected in dune areas only. Until more long term research studies such as Sevilleta LTER (Brookhart & Brantley 2000) are conducted from several widely dispersed areas conclusions as to solfugid distribution will be sketchy.

ACKNOWLEDGMENTS

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INDEX

A NEW *PETTALUS* SPECIES
(OPILIONES, CYPHOPHTHALMI, PETTALIDAE)
FROM SRI LANKA WITH A DISCUSSION ON THE
EVOLUTION OF EYES IN CYPHOPHTHALMI

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ABSTRACT. A new species of Cyphophthalmi (Opiliones) belonging to the Sri Lankan genus *Pettalus* is described and illustrated. Characterization of male and female genitalia and SEM illustrations are included, representing the first such analysis for the genus. This constitutes the first species of *Pettalus* to be described since 1897, although information on other morphospecies recently collected in Sri Lanka indicates that the number of species on the island is much higher than previously thought. The presence of eyes in pettalids is illustrated for the first time and the implications of the presence of eyes outside of Stylocellidae are discussed.

Keywords: Gondwana, *Pettalus lampetides*, Sri Lanka

A dearth of collections and plentitude of mysteries have long been the hallmarks of the cyphophthalmid fauna of Sri Lanka, arguably the most enigmatic among this suborder of Opiliones. Only two species—the first one originally assigned to the genus *Cyphophthalmus*—have been formally recognized, both over two centuries ago: *Pettalus cimiciformis* (O. Pickard-Cambridge 1875) and *P. brevicauda* Pocock 1897. The former species was described from a single male specimen collected in an unspecified locality in "Ceylon", and the latter from an adult male and a male juvenile collected in Pundaluoya (specimens deposited at the BMNH). All three specimens, collected in the 19th century, feature a peculiar modification of the terminal opisthosomal tergites that forms the "tail" characteristic of male *Pettalus*.

Subsequent to the original descriptions (O. Pickard-Cambridge 1875; Pocock 1897), Hansen & Sørensen (1904) undertook redescription of the anatomy of the specimens for their monograph. However, the original descriptions conflict significantly with those of Hansen & Sørensen (1904), possibly because the two species were confused with each other

during redescription. Study of the specimens of *P. brevicauda* was not resumed until two recent cladistic analyses of the cyphophthalmid genera (Giribet & Boyer 2002) [these specimens are referred to, erroneously, as *P. cimiciformis* in this publication, following redescription by Hansen & Sørensen (1904)] and specifically of the family Pettalidae (Giribet 2003). Due to the paucity of available specimens known until the publication of these articles, SEM studies and details of the genitalia of the genus *Pettalus* have heretofore not been undertaken.

An entomological research expedition to Sri Lanka in 1970 by collectors Claude Besuchet and Ivan Löbl led to the collection of 75 *Pettalus* specimens currently deposited at the Muséum d'histoire naturelle, Ville de Genève, which have never been previously studied. Preliminary analysis of these specimens has revealed eight morphospecies, which differ considerably from the two previously described species of *Pettalus*. Here we describe the first new species belonging to the genus *Pettalus* from that collection, and for the first time provide details of the genitalia and SEM studies for the genus. The new species is smaller than the two previously described species. It is, however, not the smallest species collected, as pending descriptions will clarify.

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This constitutes the first report and description of a species belonging to *Pettalus* since 1897.

METHODS

Abbreviations.—Specimens are lodged in the following institutions: BMNH = The Natural History Museum, London (UK); MCZ = Museum of Comparative Zoology, Harvard University, Cambridge (USA); MHNG = Muséum d'histoire naturelle, Ville de Genève (Switzerland). Nomenclature on cuticular ornamentation follows Murphree (1988). One male and one female specimen were examined with a Scanning Electron Microscope (SEM) FEI Quanta 200. The holotype was photographed in dorsal, ventral and lateral positions using a JVC KY-F70B digital camera mounted on a Leica MZ 12.5 stereomicroscope. A series of images (from 10 to 15) were taken at different focal planes and assembled with the dedicated software package Auto-Montage Pro Version 5.00.0271 by Syncroscopy. All measurements are given in mm, unless otherwise indicated.

TAXONOMY

Family Pettalidae Shear 1980
Genus *Pettalus* Thorell 1876

Pettalus Thorell 1876: 469.

Type species.—*Cyphophthalmus cimiciformis* O.P.-Cambridge 1875, by monotypy.

Pettalus lampetides new species
(Figs. 1–24)

Type material.—SRI LANKA: *Province of Uva*: male holotype, Diyaluma Falls [ca. 6°44'N, 81°01'E], 25 January 1970, C. Besuchet and I. Löbl (MHNG). Paratypes: 5 males, 2 females, same collecting data as holotype (MHNG); 1 male, 1 female (for SEM) same collecting data as holotype (MCZ 62997, 62998); 1 male, 1 female, same collecting data as holotype (MCZ 62999).

Additional material studied.—SRI LANKA: *Province of Uva*: 10 juveniles, same collecting data as holotype (MHNG). At least one large juvenile belongs to a different species, and therefore we cannot confidently assign the juveniles to *P. lampetides*.

SRI LANKA: *Central Province:* Pundaluoya [ca. 7°02'N, 80°40'E], type specimens of *Pettalus brevicauda* (BMNH).

Etymology.—The specific epithet refers to

the mythological character that was killed by the warrior Pettalus in Ovid's Metamorphoses, Book Five (Ovid, trans. 2004).

Diagnosis.—Small pettalid with distinct bilobed terminal opisthosomal tergite. Ozophores of type 3. Eyes present. Chelicerae of protruding type, proximal article with dorsal and ventral crest, and double cheliceral dentition. Palpal trochanter without ventral process. First and second coxae of walking legs free, third coxae fused to fourth. Adenostyle lamelliform, in most-proximal region of tarsus IV. Spiracles in the shape of an open circle. Sternal opisthosomal glands absent. Sternites 8 and 9 and tergite IX free, not forming a corona analis. Male and female lacking anal glands and modifications of anal region. Penis short, of microtrichal formula 2–6–8, with two movable fingers in gonopore complex. Ovipositor, composed of two apical lobes and 28 circular articles; three terminal articles before apical lobe longer than reminder articles; setae on third terminal article longer than those on more proximal articles; setae on the two terminal articles much longer. Each apical lobe carrying several setae, including a long terminal seta and a multibranched sensitive process.

Description.—Total length of male holotype (one female paratype from MHNG in parentheses) 2.48 (2.62), width across ozopores 0.88 (0.86), greatest width 1.44 (1.48), equally wide on widest part of prosoma and on second abdominal segment (Fig. 1); length-width ratio 1.72 (1.78).

Body orange to reddish brown (when preserved in ethanol) depending on incidence of light. Body almost entirely covered by a dense tuberculate-granulate microstructure. Anterior portion of prosoma tapering towards the anterior margin where the chelicerae insert (Fig. 1). Eyes present (Figs. 10–11). Ozophores conical, of type 3 of Juberthie (1970); see a re-definition of the types of ozophores in Giribet (2003) (Figs. 1, 2, 11). Transverse opisthosomal sulci conspicuous (Fig. 1). Mid-dorsal longitudinal opisthosomal sulcus absent (Fig. 1). Posterior end of the opisthosomal region clearly bilobed in males as a result of an extension of tergite VIII, which tapers, forming the characteristic tail of the genus (Figs. 1–4); tergites VI to VIII clearly concave (Fig. 2). Dorsal part of tergite VIII covered with a high concentration of setae (scopula); ventral
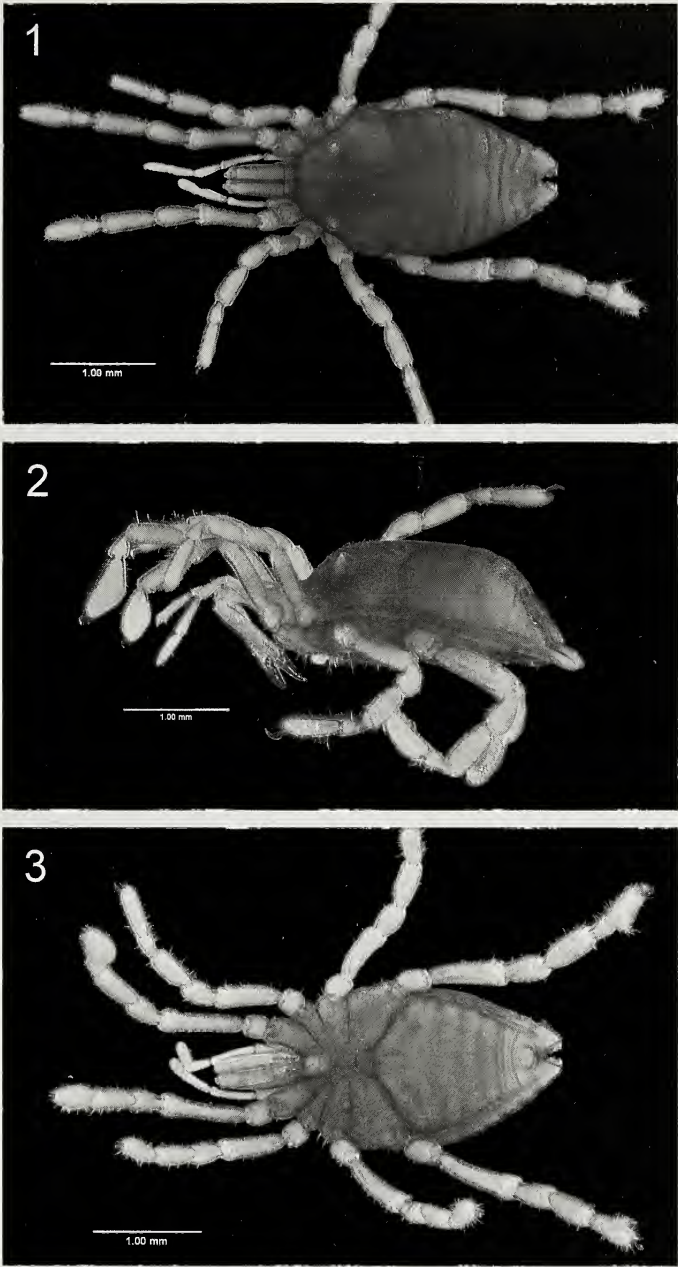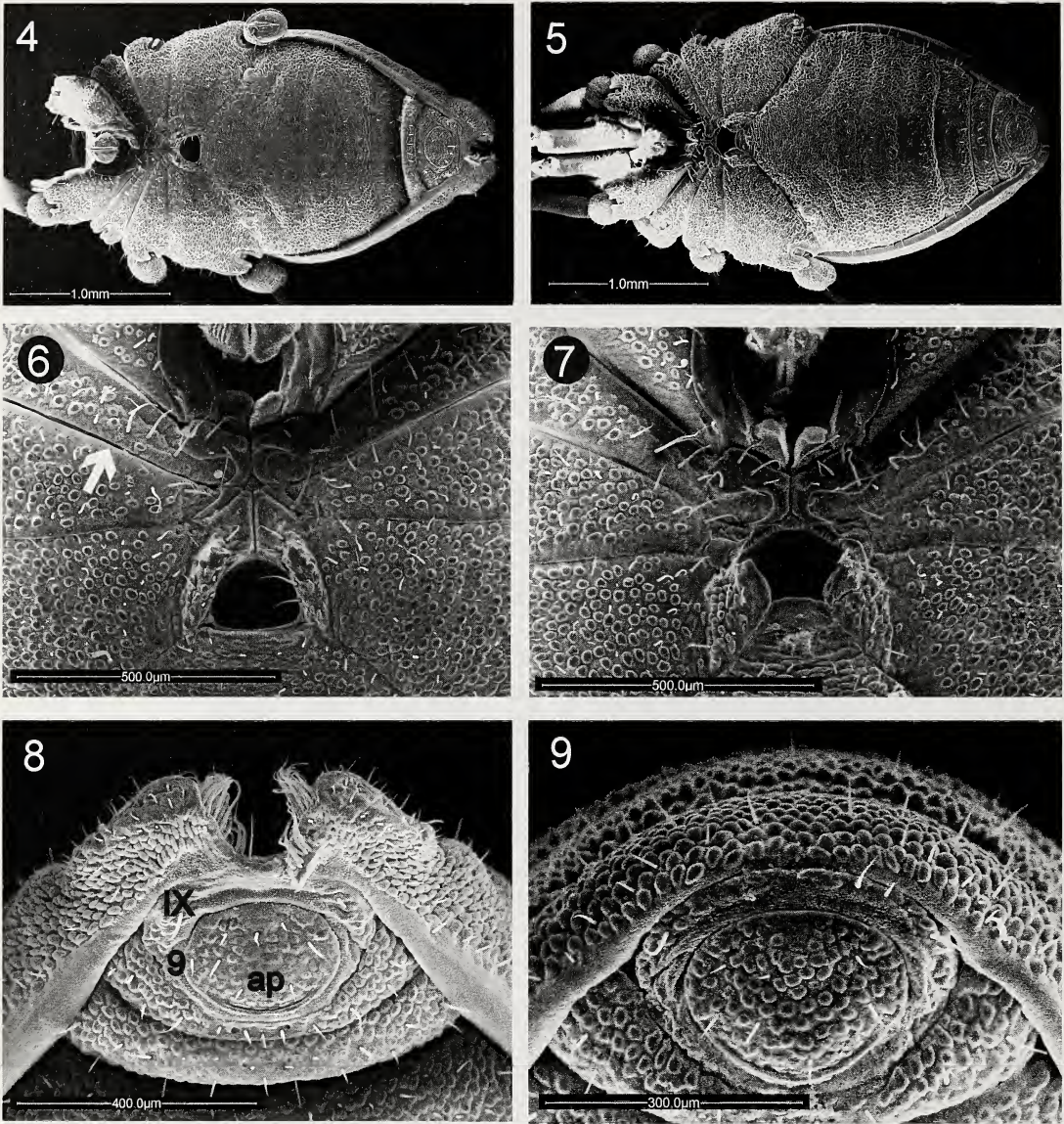
Figures 1–3.—*Pettalus lampetides* new species: 1. Dorsal view of male holotype; 2. Lateral view of male holotype; 3. Ventral view of male holotype.

side only with cuticular ornamentation, without setae (Figs. 1, 3, 4, 8). Female posterior opisthosomal region without clear modifications (Figs. 5, 9).

Coxae of legs I and II movable, coxae of legs III and IV fused. Ventral prosomal complex of male with coxae of legs II and IV meeting in the midline, but coxae I and III not

so (Fig. 6). Pore of coxal gland opening between coxae III and IV (Fig. 6). Sternum absent. Gonostome sub-semicircular, approximately as long as wide; lateral walls formed by elevated endites of coxae IV. Ventral prosomal complex of female with only coxae II meeting in the midline (Fig. 7). Spiracles typical of pettalids, in the form of an open circle
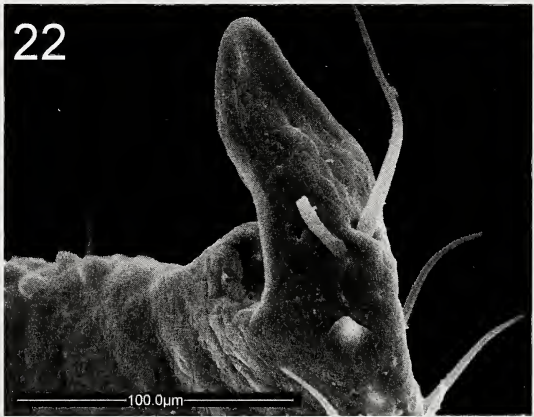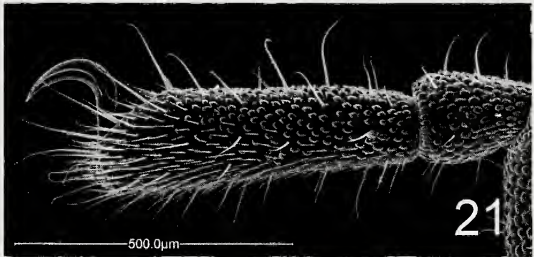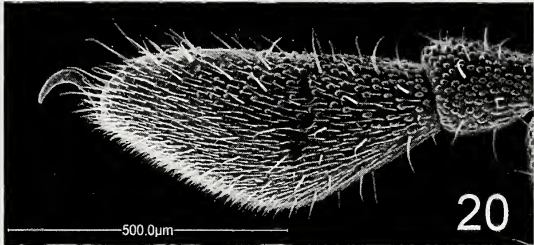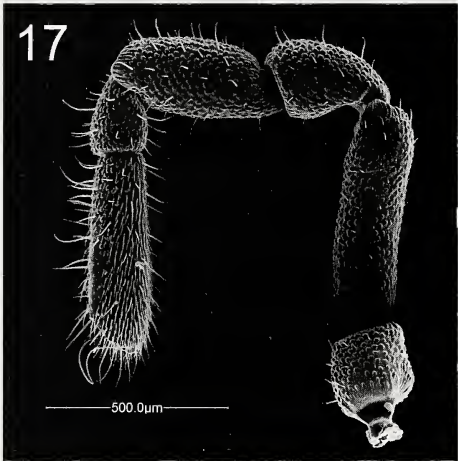
Figures 4–9. *Pettalus lampetides* new species: 4. Ventral view of male paratype; 5. Ventral view of female paratype; 6. Sternal region of male paratype; 7. Sternal region of female paratype; 8. Anal region of male paratype showing the anal plate (ap) and sternite 9 embedded by tergite IX; 9. Anal region of female paratype.

(Fig. 12), opening towards the postero-lateral side. Sternal opisthosomal glands absent. Sternites 8 and 9 and tergite IX free in males and females, not forming a corona analis (Figs. 8–9). Relative position of sternite 9 and tergite IX of pettalid type, sensu Giribet & Boyer (2002), where the sternite is embedded by the tergite. Anal plate without modifications, in ventral position in males and females (Figs. 8–9). Anal plate 0.18 (0.19) long and 0.27 (0.27) wide. Anal gland pores absent (Figs. 8–9).

Chelicerae (Fig. 13) of protruding type, with the dorsal crest clearly visible from above (Fig. 1); relatively slender; with few setae. Granulation restricted to the proximal article covering almost the entire surface, but not the most-distal portion. Proximal article of male and female paratypes examined by SEM 0.97 (0.90) long, 0.36 (0.35) deep, with con-
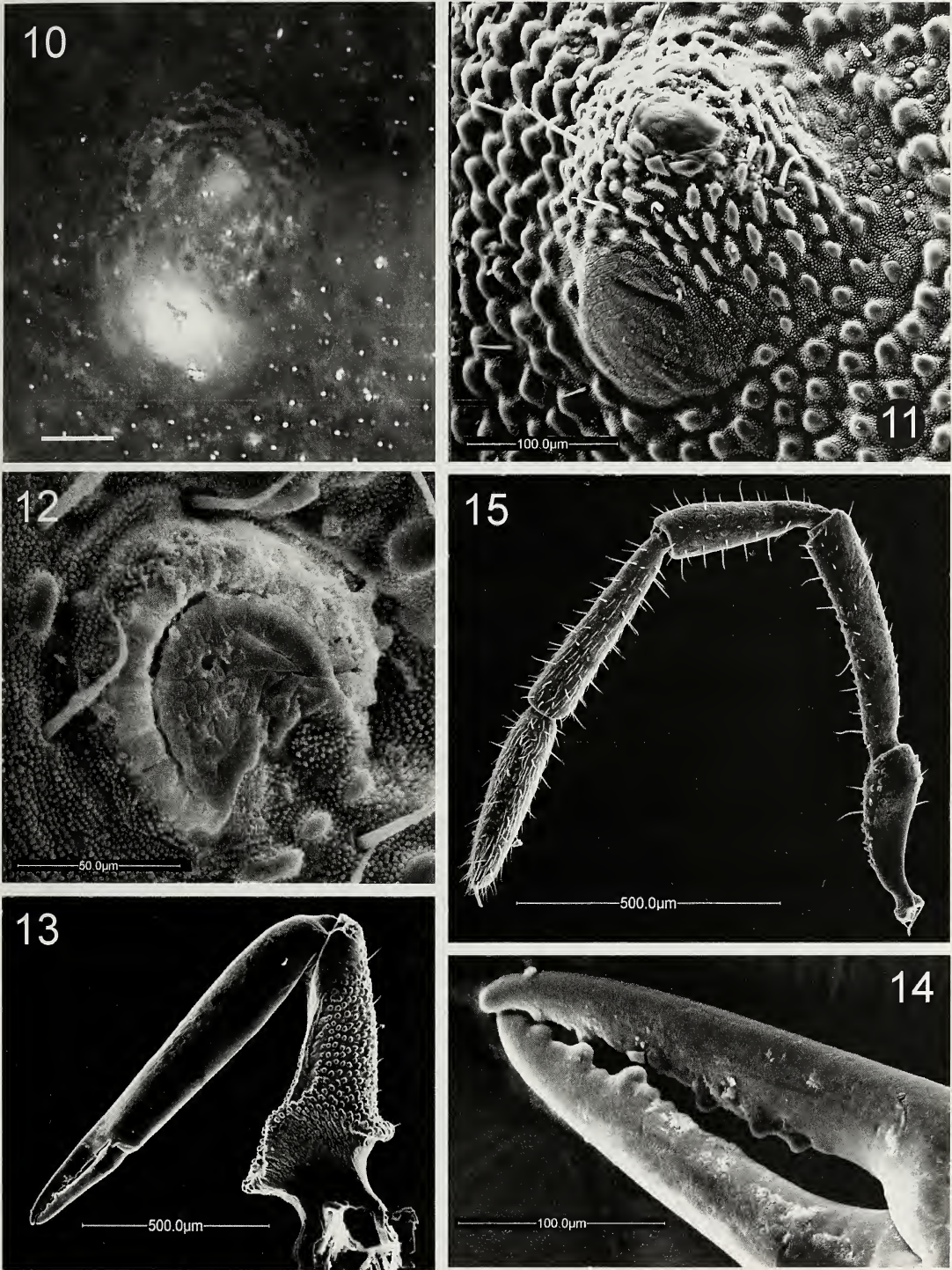
Figures 10–15. *Pettalus lampetides* new species: 10. Left eye and ozophore of female paratype examined by light microscopy (scale bar = 50 μm); 11. Left eye and ozophore of male paratype examined by SEM; 12. Spiracle of male paratype; 13. Lateral view of left chelicera of male paratype showing dorsal and ventral crests; 14. Detail of the dual dentition of the cheliceral distal segments; 15. Left palp of male paratype.
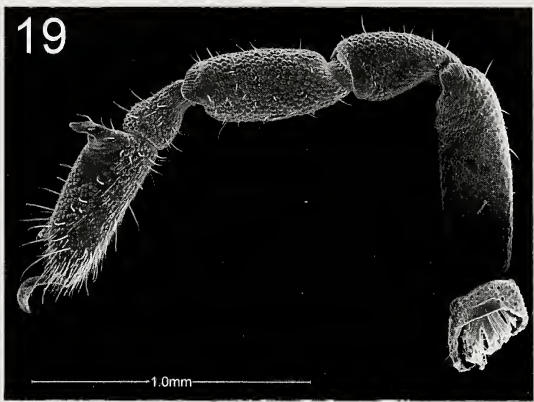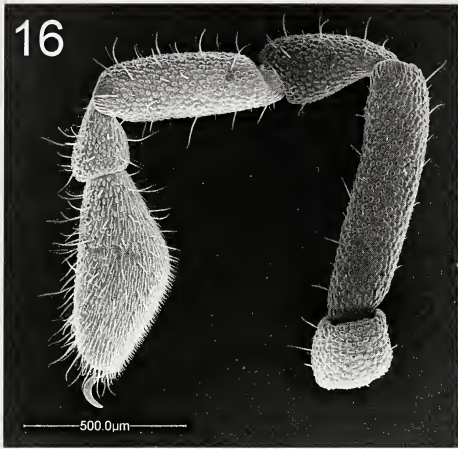
Figures 16–22. *Pettalus lampetides* new species: 16. Male left leg I; 17. Male left leg II; 18. Male left leg III; 19. Male left leg IV; 20. Detail of male left tarsus I; 21. Female left tarsus IV; 22. Detail of adenostyle.

Table 1.—Leg measurements in mm for paratypes of *Pettalus lampetides* examined by SEM (MCZ 62997, 62998). Data represent male/female values and (ration of the sexes).

	Tr	Fe	Pa	Ti	Mt	Ta	Total
Leg I	0.21/0.25 (0.84)	0.73/0.20 (3.7)	0.42/0.22 (1.9)	0.50/0.21 (2.4)	0.26/0.18 (1.4)	0.57/0.28 (2.0)	2.69
Leg II	0.22/0.23 (0.96)	0.56/0.18 (3.1)	0.34/0.22 (1.6)	0.39/0.22 (1.8)	0.25/0.16 (1.6)	0.46/0.17 (2.7)	2.22
Leg III	0.22/0.26 (0.85)	0.57/0.22 (2.6)	0.35/0.23 (1.5)	0.41/0.24 (1.7)	0.24/0.16 (1.5)	0.39/0.19 (2.1)	2.18
Leg IV	0.30/0.31 (0.97)	0.72/0.26 (2.8)	0.45/0.25 (1.8)	0.51/0.27 (1.9)	0.28/0.18 (1.6)	0.48/0.24 (2.0)	2.74
Leg I	0.17/0.26 (0.65)	0.69/0.69 (3.5)	0.38/0.22 (1.7)	0.44/0.20 (2.2)	0.25/0.17 (1.5)	0.52/0.25 (2.1)	2.45
Leg II	0.19/0.21 (0.90)	0.51/0.51 (2.6)	0.32/0.22 (1.5)	0.35/0.21 (1.7)	0.21/0.16 (1.3)	0.36/0.16 (2.3)	1.94
Leg III	0.22/0.23 (0.96)	0.54/0.54 (2.8)	0.33/0.21 (1.6)	0.38/0.21 (1.8)	0.24/0.15 (1.6)	0.43/0.15 (2.9)	2.14
Leg IV	0.29/0.26 (1.1)	0.74/0.74 (3.0)	0.40/0.25 (1.6)	0.48/0.24 (2.0)	0.28/0.18 (1.6)	0.50/0.18 (2.8)	2.69

spicuous dorsal crest that extends ventrally but without forming a ventral process, and single posterior ventral process. Second article 1.17 (1.15) long, 0.18 (0.17) deep, subcylindrical, its widest portion towards the first third of its length; dentition irregular. Distal article 0.31 (0.31) long, 0.05 (0.05) deep, with the two types of dentition typical of pettalids (Fig. 14).

Palp (Fig. 15) without ventral process in trochanter; without conspicuous modifications. Length/width (length-width ratio in parentheses) of palpal articles from trochanter to tarsus of male paratype examined by SEM [of female paratype in square brackets]: 0.32/0.12 (2.8) [0.32/0.10 (3.2)]; 0.47/0.09 (5.2) [0.47/0.09 (5.2)]; 0.32/0.1 (3.2) [0.32/0.09 (3.6)]; 0.42/0.09 (4.7) [0.39/0.09 (4.3)]; 0.36/0.09 (4.0) [0.35/0.09 (3.9)]; total length 1.86 [1.84]. Palpal claw 0.04 (0.04) long.

Legs (Figs. 16–21) with all claws smooth, lacking dentition or lateral pegs. Surfaces of all trochanters, femurs, patellae, tibiae and metatarsi granulated. Granulation of all tarsi concentrating in the dorsal side. Tarsus I with a distinct solea (Figs. 16, 20).

Leg measurements of male and female paratypes examined by SEM are provided in Table 1: length/width (length-width ratio in parentheses). Tarsus IV of males not divided, carrying a lamelliform adenostyle in most proximal region of tarsus (Fig. 19). Adenostyle of male paratype examined by SEM 0.11

long (Fig. 22). Tarsus IV of female without modifications (Fig. 21).

Penis (Figs. 23–25) short, typical of pettalids. Microtrichal formula 2–6–8 (one penis studied). Dorsal side of penis with a group of eight long microtrichia on each side, with bases arranged in a "V" and not fused. Rounded distal margin of penis with six apical microtrichia, and two short microtrichia adjacent ventrally. Gonopore complex with two distinct movable fingers in the shape of curved hooks.

Ovipositor (Figs. 26–27) long, composed of two apical lobes and 28 circular articles (one ovipositor studied), each of the latter furnished with 8 equally long setae. Three terminal articles before apical lobe longer than reminder articles; setae on third terminal article longer than those of more proximal articles; setae on the two terminal articles much longer. Each apical lobe carrying several setae, including a long terminal seta and a sensitive process with a multibranched seta (Fig. 27).

Variation.—Range of measurements in males ($n = 8$) and females ($n = 4$; in parentheses): Body length 2.36–2.58 (2.62–2.70), maximum (and anterior) width 1.40–1.50 (1.42–1.50).

Distribution.—Known only from the type locality. A recent expedition in June 2004 by the authors to Diyaluma Falls did not result in new specimens of this species.

Remarks.—*Pettalus lampetides* is consid-
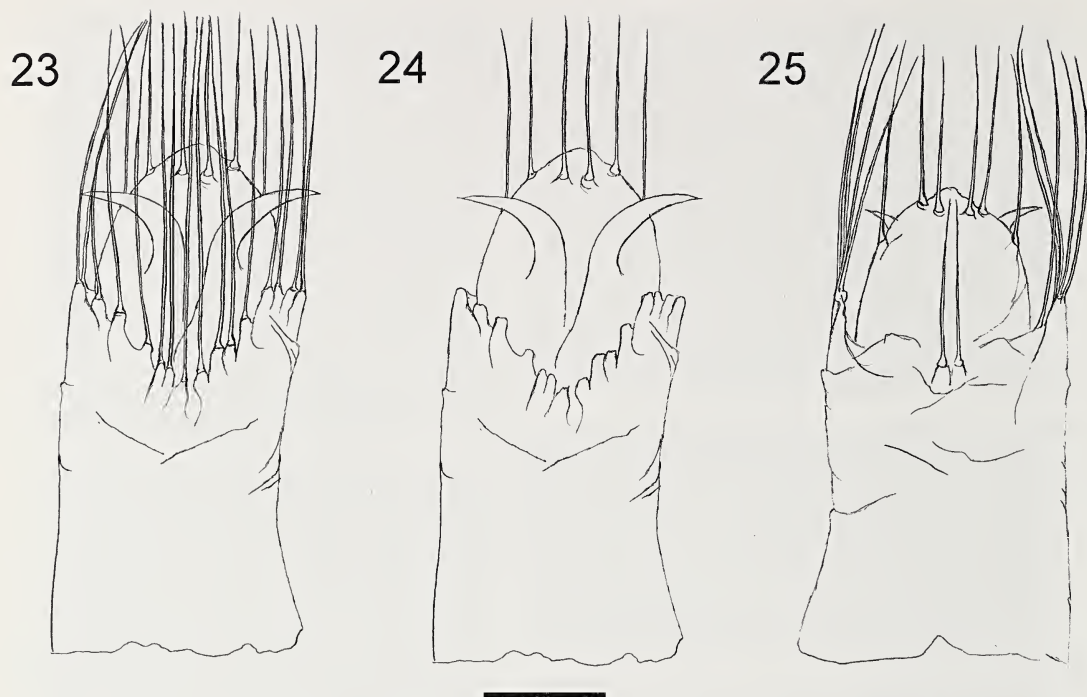
Figures 23–25. *Pettalus lampetides* new species: 23. Total penis, dorsal view; 24. Dorsal view showing apical microtrichia and movable fingers; 25. Ventral view. Scale bar = 125 μm.

erably smaller than the other two described species of *Pettalus*. In comparison with *P. brevicauda*, the "tail" extension of *P. lampetides* is much shorter and less conspicuous. In lateral view *P. brevicauda* tapers starting from the first opisthosomal segments, whereas *P. lampetides* tapers more abruptly beginning in the middle of the opisthosoma (Fig. 2). The tail of *P. brevicauda* is globose, whereas that of *P. lampetides* is flat. Finally, the chelicerae of *P. lampetides* are of the protruding type, where the dorsal crest does not articulate with the anterior margin of the carapace, whereas in *P. brevicauda* the dorsal crest articulates with the anterior part of the carapace while in resting position.

DISCUSSION

Pettalus lampetides clearly belongs to the genus *Pettalus* on the basis of the apomorphic modification of the terminal opisthosomal tergites forming a "tail" shared by the previously described species of *Pettalus*. In addition, the typically double cheliceral dentition, ozophore type, and male genitalia support its placement in the family Pettalidae. Due to the age of the available collection and the lack of

recently collected specimens in the aforementioned expedition in June 2004, molecular analysis of specimens was not attempted at this time.

Despite the paucity of described *Pettalus* species, as many as ten new species may be available for description and study in the collections from the 1970 MHNG expedition and 2004 MCZ expedition. A third collecting trip by S. Mahunka & L. Mahunka-Papp yielded one female specimen deposited at the Hungarian Natural History Museum (Budapest). The occurrence of these species in a relatively small area suggests significant diversity of cyphophthalmid fauna in Sri Lanka. Due to the small size and leaf-litter habitat of most cyphophthalmid species, it is probable that additional species could be discovered in the subcontinental region. Studying this fauna could be of extreme importance not only for characterizing a putative radiation in Sri Lanka, but also for biogeographical studies of Gondwanan fauna.

Evolution of Eyes in Cyphophthalmi.— From the 140 species and subspecies described to date in the Opiliones suborder
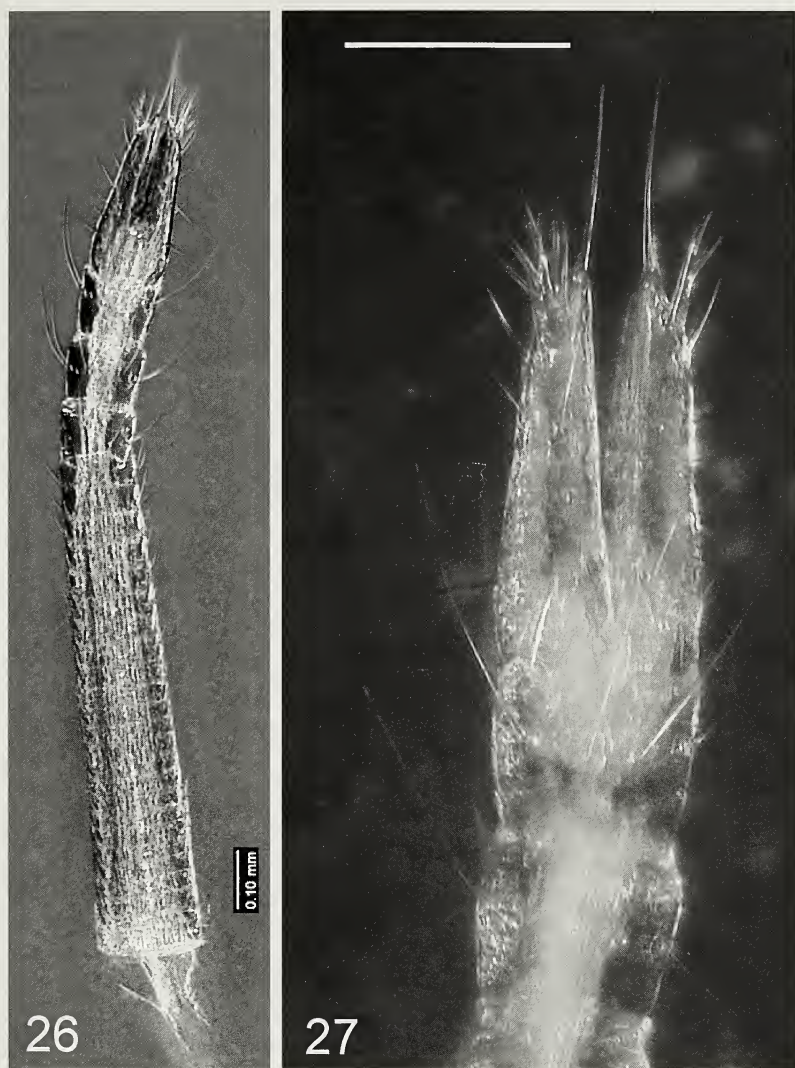
Figure 26–27. *Pettalus lampetides* new species: 26. Total ovipositor, dorsal view; 27. Detail of ovipositor tip (scale bar = 156 μm).

Cyphophthalmi (see online catalog of Cyphophthalmi at http://collections.oeb.harvard.edu/Invertebrate/Cyphophthalmi/species.cfm), only those of the genus *Stylocellus* (family Stylocellidae) were so far known to have eyes (Hansen & Sørensen 1904; Shear 1980; Giribet & Boyer 2002; Giribet et al. 2002). All described members of the five remaining families are eyeless. However, in his description of *Austropurcellia scoparia* Juberthie (1988: 133) reported the presence of an undescribed species of *Neopurcellia* with eyes from a batch of eleven new species collected in Queensland (Australia) and borrowed from Valerie Todd Davies (Queensland Museum, Brisbane). The existence of a pettalid with eyes was again mentioned by Rambla and Juberthie (1994), but ignored in subsequent papers by Juberthie, including descriptions of new species from Queensland (Juberthie 1989, 2000). However, the title of Juberthie's paper of 2000 once more seems to refer to the presence of eyes in pettalids by specifically mentioning the blindness of the new species: "A new blind Cyphophthalmi (Opiliones) from Queensland (Australia)". Why would anyone describe a pettalid species as a "blind Cyphophthalmi" when all known members of this family (and most other cyphophthalmids) are blind? Due to the lack of physical proof,

the citation in Juberthie (1988) and the odd title of his 2000 description were regarded as questionable (Giribet 2003). However, the implications of the presence of eyes in pettalids could be of fundamental importance for reconstructing the common ancestor of Cyphophthalmi and the phylogeny of Opiliones.

Stylocellids are currently considered to be the sister group to all other cyphophthalmids (Giribet & Boyer 2002). Due to the questionable homology of eyes in Cyphophthalmi and in other Opiliones, and due to the apparent lack of eyes in one of the two clades of Cyphophthalmi (which comprises five of the six families currently recognized), it was equally parsimonious to reconstruct the common ancestor of Cyphophthalmi with or without eyes. However, if eyes homologous to those of stylocellids were found in its sister clade—as reported by Juberthie (1988)—it would be most parsimonious to infer a cyphophthalmid ancestor with eyes.

The new species of *Pettalus* described here is interesting in that—like the *Neopurcellia* mentioned by Juberthie (1988)—it has eyes. Re-examination of the older species of *Pettalus* as well as all new specimens deposited at the MCZ or the MHNG shows that all Sri Lankan pettalids have eyes. These are located at the base of the type 3 ozophores (Figs. 10–11) and clearly show a transparent cornea. The eyes resemble those of stylocellids, but they are incorporated into the base of the ozophores, while in stylocellids the eyes are located anterior to, and not incorporated into, the ozophores.

The discovery of eyes in this pettalid is truly remarkable, but certainly not an exception. Re-study of species from other genera has shown that eyes may be more widespread within pettalids than previously thought, as they are also present in *Chileogovea* (see de Bivort & Giribet 2004: fig. 11j). Therefore, at least four previously described species of pettalids have eyes, even though they had not been noticed by previous authors during more than 135 years of knowledge of these pettalids. In addition, the Indian cyphophthalmids reported by Bastawade (1992) also bear eyes like those of stylocellids.

Arachnids typically have a pair of median eyes and a variable number of lateral eyes (Paulus 1979; Weygoldt & Paulus 1979; Giribet et al. 2002). Opiliones remain a mystery

because most Phalangida (the non-cyphophthalmid Opiliones) bear a pair of median eyes (sometimes these migrate laterally as in the biantid-like families, and in Stygnidae and some Epedanidae) whereas the eyes present in some Cyphophthalmi are thought to be homologous to the lateral eyes of other arachnids (Shear 1993; Giribet et al. 2002), but other opinions exist. Hansen & Sørensen (1904: 35) maintained that the eyes of *Stylocellus* correspond morphologically to the pair of median eyes in other Opiliones. However, the presence of eyes in only some members of a single family of Cyphophthalmi, i.e. Stylocellidae, questioned the true homology of cyphophthalmid eyes, because, if they were not homologous to the median eyes of Phalangida, they could be apomorphic for the genus *Stylocellus*. The presence of eyes in some members of the sister clade of Stylocellidae suggests that eyes may have been present in the common ancestor of all Cyphophthalmi and, therefore, strengthens the case for homology.

ACKNOWLEDGMENTS

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CYTOCHEMICAL STUDIES OF RNA AND BASIC NUCLEAR PROTEINS IN LYCOSID SPIDERS

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ABSTRACT. Tissues of lycosid spiders were studied for RNA distributions with the basic dye Azure B. Changes in the basic proteins associated with DNA during spermiogenesis were identified with alkaline fast green staining after DNA extraction with trichloroacetic acid and by cytochemical tests for arginine. Tissue glycoproteins of the gut diverticula and the ducts of silk glands were resistant to diastase digestion and required periodic acid hydrolysis to localize reaction products with the Schiff reagent for aldehydes. Spiders possess novel types of cells that are in need of further study and may be useful as models for developmental biology.

Keywords: Araneidae, RNA, histone proteins, protamines, spermiogenesis

In conjunction with studies of polyploidization in lycosid and araneid spiders (Rasch & Connelly 2004), a number of standard cytochemical procedures were used to identify RNA, histone and non-histone nuclear proteins in several organ systems of lycosid spiders. Aside from the recent cytological studies in several species of spiders from Taiwan (Chen 1999) and the quantitative determination of genome sizes for 115 species of spiders by image analysis densitometry (Gregory & Shorthouse 2003), there have been few general studies of arachnid cytochemistry since the early reports by Millot (1926, 1949) on the histophysiology of many different types of cells from several species of spiders and the reports on the cytochemistry of silk glands of mygalomorph spiders by Palmer et al. (1982) and Palmer (1985). The most recent reviews of the microscopic anatomy of spiders are those by Felgenhauer (1999) and the excellent descriptions of the fine structure of major organ systems by Foelix (1996). Both are comprehensive in their coverage and emphasize the sometimes unique adaptations of cells to the particular life style of these carnivorous animals. The present study is a brief description of the cytomorphology and nucleoprotein cytochemistry of several lycosid spiders. It points out that these understudied animals have many interesting and novel types of cells that may be useful for future studies of invertebrate tissue development and cell differentiation.

METHODS

Tissue imprints were obtained as touch preparations from the severed prosoma and abdomens of 1 male and 3 females of undetermined medium-sized members of the family Lycosidae collected from a small wooded lot in Johnson City TN (36.2923 latitude and −82.3773 longitude). Specimens were immobilized by chilling at 4 °C for 30 min before sacrifice. Bodies were separated at the pedicel and touched to a glass slide to obtain one or two droplets (1–3 μl) of hemolymph. Severed abdomens were routinely fixed for 3–4 hr in 3:1 methanol/acetic acid (v/v), dehydrated and embedded in PolyFin (Polysciences Inc., Warrington PA). Others were fixed for 3–4 hrs in 10% neutral formalin or in MFA (methanol/formalin/acetic acid; 85:10:5, v/v) and washed overnight in tap water before dehydrating, embedding and sectioning in the usual manner at 8 μm with an A&O Model 820 rotary microtome. Block faces varied between 3–7 mm in diameter. Serial sections were mounted on albumen-coated slides for routine staining with Harris hematoxylin and eosin, or for processing through the cytochemical procedures outlined below.

Tissue samples of testes of rainbow trout (*Onchorynchus mykiss*) and 6 month-old cat (*Felix domesticus*), for which cytochemical

staining reactions for basic nucleoproteins are well recognized (Alfert & Gescshwind 1953; Rasch & Woodard 1959), were fixed in 10% neutral formalin and processed as above for tissue sections. Chicken blood smears (*Gallus domesticus*) were also used as a representative reference tissue for evaluating acid extraction procedures and thereby establishing an operational definition for histone proteins and protamines (Alfert 1956). All cytochemical reactions on spider tissues were applied in sequence to sections which had been part of the same paraffin ribbon in order to minimize differences due to variations in the fixation history of tissue blocks. Slides of the reference tissues were routinely processed simultaneously with each set of spider tissues.

RNA staining.—The RNA/DNA staining procedure of Flax & Himes (1952) was modified to stain sectioned spider tissues in a 0.025% solution of Azure B bromide (C.I. 52010) in 0.01 M acetate buffer at pH 4.0–4.1 for 2 hr at 37 °C. After a brief rinse in distilled water to remove excess dye, slides were dehydrated quickly through 3 rinses of tertiary butyl alcohol (TBA) for 2–3 min in each change and then allowed to stand overnight in a fresh change of absolute TBA before clearing in xylene and mounting in immersion oil or plastic resin for viewing and photography.

Basic protein staining.—All slides in each experiment were treated simultaneously through the staining procedures described by Alfert & Geschwind (1953). Briefly, deparaffinized slides were rehydrated through graded ethanols, immersed for 1 min in distilled water at 90 °C and transferred immediately into 5% trichloroacetic acid (TCA) at 90 °C for 15 min. Following 3 rinses in chilled 70% ethanol, slides were given 2 changes in distilled water and placed for 1–2 min in distilled water at pH 8.1 before being placed in a freshly prepared 0.1% solution of fast green FCF (C.I. 42053) adjusted to pH 8.1 with a minimum amount of 1 N NaOH. After staining for 60 min, slides were quickly dipped in 2 changes of distilled water at pH 8.1 and then dehydrated rapidly through 3 changes of TBA and cleared in xylene. Specificity of the staining for basic proteins was verified by carrying matching slides through a distilled water bath at 90 °C while test slides were hydrolyzed in 5% TCA and then staining all slides simulta-

neously in the same fast green solution at pH 8.1. Controls included slides of chicken RBC nuclei, trout RBC nuclei and slides carrying sections of testis from rainbow trout and domestic cat to assess conversion from histone proteins to protamine-like proteins during sperm maturation (Alfert 1956). Replicate slides with or without the 5% hot TCA extraction were stained to confirm DNA extraction, using the Feulgen reaction for DNA as described elsewhere (Rasch 2003).

A modified protocol of the Sakaguchi histochemical reaction for arginine (Barka & Anderson 1965) was used to assess alteration of histone proteins to arginine-rich protamines during spermiogenesis in lycosid spiders. The procedure described by Rasch & Woodard (1959), required the incubation of deparaffinized and rehydrated sections for 3 min at 23 °C in 0.5% 8-hydroxyquinoline (Eastman Kodak) in absolute ethanol, followed by development of a bright orange reaction product within 30–45 sec in a 1:1:1 mixture of 10% NaOH, commercial Chlorox® and distilled water. The latter step was carried out at 0–1 °C in an ice bath. Preparations were immediately rinsed for 3–5 sec with 2 changes of ice-cold distilled water to remove the NaOH and dehydrated rapidly through 3 changes of TBA, cleared in 3 changes of xylene and air-dried or mounted in immersion oil for photography. Slides of chicken and trout RBC nuclei and sections of trout and cat testis were stained by the same protocol to serve as reference controls.

Periodic acid Schiff reaction (PAS).—Carbohydrate and glycoprotein deposits in sections of spider abdomens were localized by hydrolysis for 10 min in 0.5% periodic acid in distilled water, followed by a 10 min wash in running tap water and 15 min of staining in freshly prepared 1% Schiff reagent. After three 5 min rinses in sulfite water, another 10 min wash in running tap water and dehydration through absolute ethanol, preparations were air-dried and mounted in oil or resin. Matching preparations were pretreated with diastase or held in distilled water during the acid hydrolysis to serve as negative controls. All slides were stained simultaneously with the Schiff reagent and counterstained with 0.5% fast green in 95% ethanol.
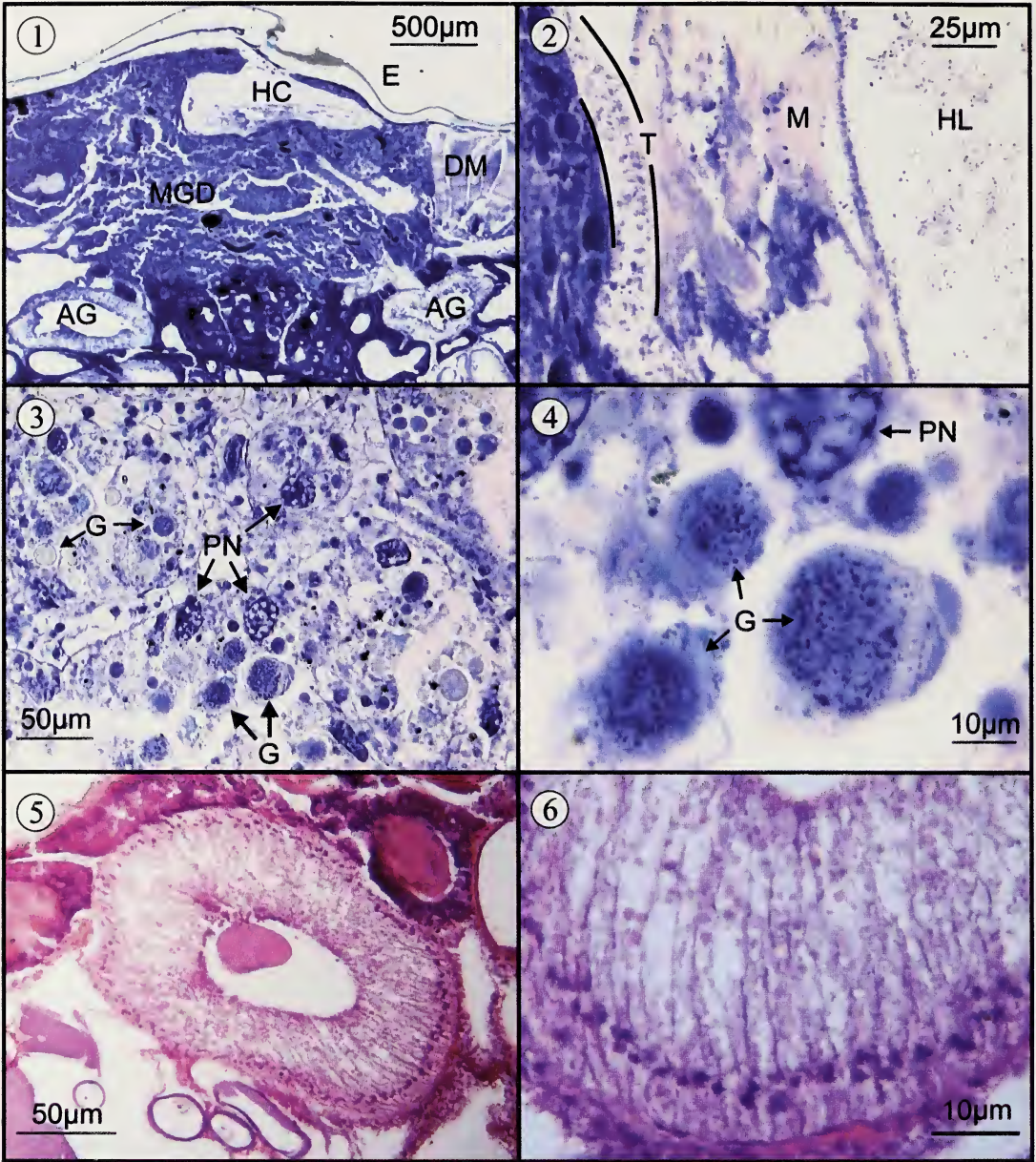
Figures 1–6.—Histological sections of lycosid spiders. 1. Low power view of x-section through the abdomen of a female wolf spider to show portions of the dorsal chitinous exoskeleton (E), heart chamber (HC), midgut diverticula (MGD), ampullate glands (AG) and dorsal muscles (DM). Azure B, pH 4.1, for RNA. 2. Periphery of heart chamber at higher magnification to show the spiral pattern of supports (at T and outlined in black) that prevent collapse of ligaments and the pericardial space during pressure changes. Note that this structure runs immediately adjacent to the heart chamber. Several tangential profiles of muscles (M) are associated with the heart. The acidophilic hemolymph (HL) is essentially unstained. Azure B, pH 4.1, for RNA. 3. Low power view of cells from the posterior of the midgut diverticula to show the densely stained networks of chromatin strands of the large polyploid nuclei (PN) characteristic of this tissue in lycosid and araneid spiders. Note the many small droplets and large, amorphous globules

RESULTS

Sections through the abdomens of lycosid females after staining with Azure B reveal large amounts of RNA basophilia present in cells of the midgut diverticula (MGD) that fill the space around and under the heart chamber, which is positioned just below the dorsal surface of the body (HC in Fig. 1). Tangential sections through the dorsal musculature (DM in Fig. 1) and the acidophilic hemolymph in the heart chamber (HL in Fig. 2) are only faintly stained. The thickened, spirally arranged reinforcements (T) that adjoin the heart chamber and its surrounding musculature also are slightly stained, possibly due to strongly acidic groups of their constituent glucosamine polymers, as is also evident in the thin walls that delimit air pockets in the book lungs (Fig. 9). At higher magnification, the polysomatic nuclei (PN) of the gastric diverticula are strongly basophilic, as are many of the small droplets and varying sizes of spherules shown in Fig. 3. These bodies are bluish pink in adjacent sections stained with hematoxylin and eosin and presumably are the zymogen granules released from secretory cells during food processing in this tissue. The vacuolate appearance of the cytoplasm of other cells is taken to reflect resorption by endocytosis and intracellular transport of digested materials. Identification of the interstitial cells that are so clearly delineated in electron micrographs (Foelix 1996) is uncertain here, probably because they are obscured by surrounding secretory and absorptive cells and lack appreciable basophilia. Some of the smaller droplets appear to be faintly azurophilic and have a homogeneous texture. Many of the larger spherules also appear to be basophilic, but the coloration is due in part to the small granules that coat the surfaces of these globules (Fig. 4). In adjacent unstained sections the large spheres are yellow to dark tan in color and are highly refractile when viewed by phase microscopy. The image in Fig. 4, when viewed at a higher magnification, shows part of a polysomatic nucleus (PN) and several large globules slightly under-focused to show the superficial caps of densely azurophilic granules in the optical plane above the spheres. The globules are resistant to extraction by ethanols, butanols, chloroform, ether, xylene, 5% trichloroacetic acid and 5 N HCl, which suggests that they consist of highly condensed and sequestered proteins that are related to enzymic processing and subsequent excretion of ingested food materials.

The ampullate silk glands of lycosid spiders are readily recognized by their size and characteristic morphology (Fig. 5). The tail portions of these glands show highly basophilic cytoplasm at the cell apex with nuclei restricted to the basal regions, as shown for higher power view of the sac of the ampullate gland (Fig. 6). Protein secretions in the lumen of both parts of the gland are strongly eosinophilic (Fig. 5).

The structure of the book lung (BL) in the abdomen of a lycosid spider is shown in Fig. 7, which was seen in the male, a portion of whose tubular testis lies adjacent to the connective tissue of the lung on the ventral surface of this animal. Several bundles of muscle (M) just above the exocuticle are evident from

←

Figures 1–6. (continued)—(G) that accumulate in this tissue during food processing and absorption. Azure B, pH 4.1, for RNA. 4. Same as in Fig. 3, at higher magnification to show part of a polyploid nucleus (PN) and several large globules (G). The image is slightly under-focused to show the superficial caps of densely basophilic granules (arrows) in the plane above the globules. The granules are resistant to extraction by ethanol, butanol, chloroform, ether, xylene and 5N HCl. Azure B, pH 4.1, for RNA. 5. Cross sectional view of ampullate gland with a portion of the tail of the gland at upper right and chitin-lined ducts at lower left. Hematoxylin and eosin. 6. High power view of epithelial cells of ampullate gland to show nuclei at the base of highly elongated cells whose vacuolate cytoplasm contains only a few small eosinophilic droplets. Hematoxylin and eosin.
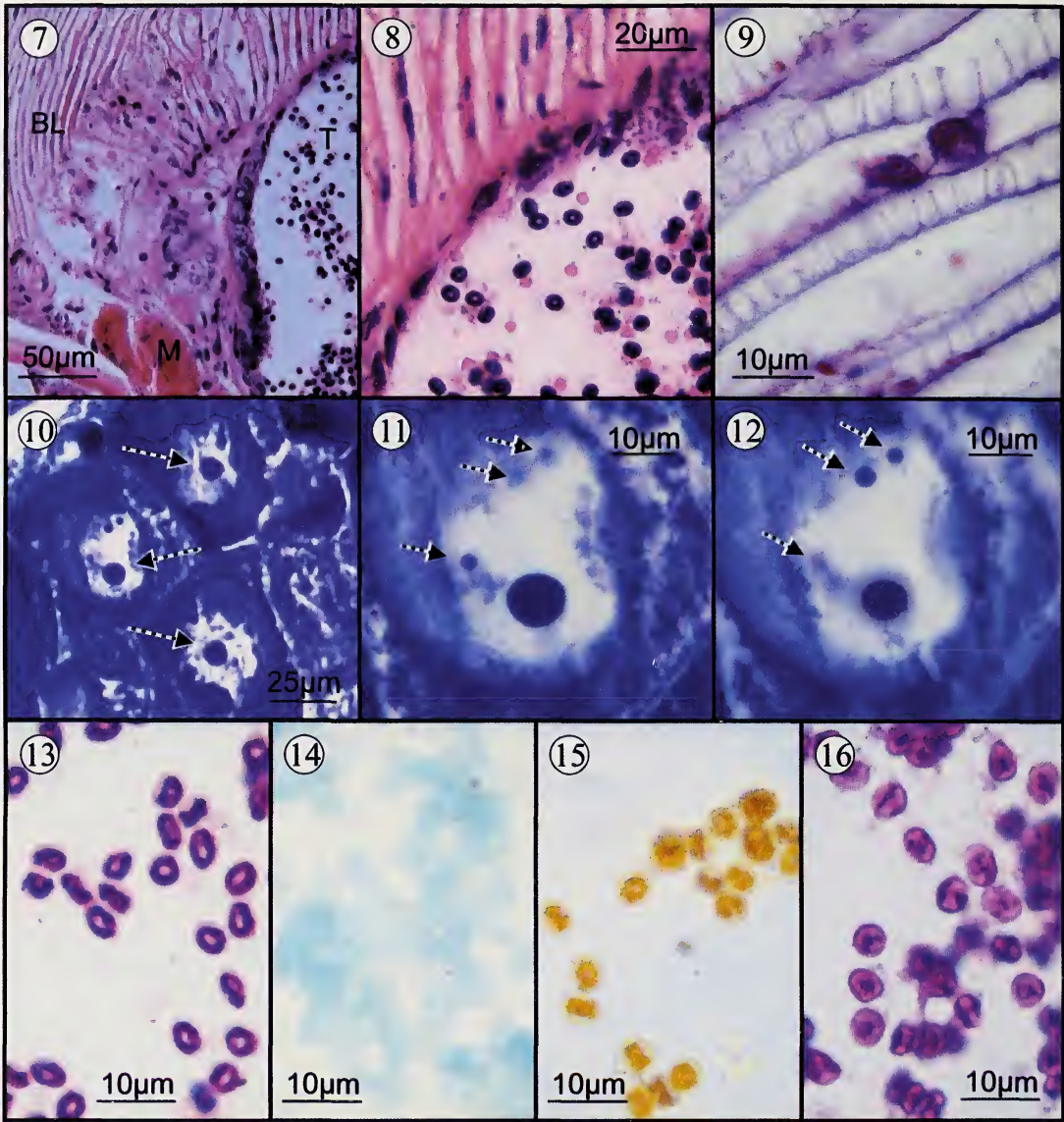
Figures 7–16.—Histological sections of lycosid spiders. 7. Low power view of a section through the abdomen of a mature male of lycosid spider to show the book lung (BL), an adjacent lobe of testis (T) and several bundles of muscle (M). Hematoxylin and eosin. 8. Same field as Fig. 7, at higher magnification to show differences in sizes, shapes and staining intensities of the nuclei of epithelial cells that separate organs, the elongated nuclei of hypodermal cells that line the air pockets of the book lungs and the small nuclei of hemocytes in the space between adjacent air spaces. Note the highly compacted, hollow centered sperm in the lumen of the testis at lower right. Hematoxylin and eosin. 9. High power view of book lung to show the oval nuclei of hemocytes in the hemolymph space between the air pockets of this tissue. Note the thin, chitinous pedestals or struts that maintain the patency of the air pockets. Periodic acid Schiff and Feulgen reactions with fast green counterstain. 10. Thick section of ovary from a young lycosid female. Note the prominent, highly basophilic nucleoli (arrows) and cytoplasm in these immature oocytes. Azure

Table 1.—Basic protein staining of spider tissue and controls with fast green at pH 8.1. Staining intensity is scored as 0 = no stain; + = trace; ++ = moderate; +++ = strong.

Treatment/Reaction	Chicken RBC	Trout RBC	Trout sperm	Cat sperm	Spider somatic	Spider sperm
Feulgen-DNA	+++	+++	+++	+++	+++	+++
Distilled water 90 °C, FG pH 8.1	0	0	0	0	0	0
Trichloroacetic acid 90 °C, FG pH 8.1	+++	+++	0	0	+++	0
Arginine	+++	+++	++	++	+++	++

their strong acidophilia after staining with hematoxylin and eosin. Fig. 8 is from the same section at higher magnification to show differences in sizes, shapes and staining intensities of the nuclei of the cells that delineate the separate organs and the slender elongated nuclei of hypodermal cells that line the air pockets of the book lungs. Both types of cells differ in size and basophilia from the small, oval nuclei of hemocytes that circulate through the hemolymph space between adjacent air pockets of the book lung (Fig. 9). All are easily distinguished from the densely stained, highly compacted, coiled sperm in the lumen of the adjacent testis (T, Fig. 7). The size of the small nuclei within the book lung is roughly equivalent to the small dark nuclei in the tangential section of the ventral musculature (M, Fig. 7). The delicate, supporting struts or pedestals of cuticle that maintain patent air passages in the book lung can be seen to good advantage after staining with the PAS reaction (Fig. 9).

Developing oocytes in the ovaries of all three lycosid females show highly basophilic staining of the cytoplasm and large, very prominent nucleoli with Azure B (Fig. 10). Many of the oocytes, however, also have up to three much smaller nucleolar bodies (Figs. 11 & 12), suggesting that there may be ribosomal gene transcription, possibly selective amplification, at more than one chromosomal site in these cells.

As shown in Fig. 8, the sperm of lycosid spiders often appear as small, densely stained rings or bars in paraffin sections, because their crescent-shaped nuclei are helically coiled in a head to tail fashion to form a nuclear bracelet or amulet that is thicker in its mid-region

Figures 7–16. (continued)—B, pH 4.1, for RNA. 11–12. High power views at different focal planes of the oocyte that is marked by the middle arrow in Fig. 10 to show a single, large primary nucleolus and three smaller nucleoli in the same nucleoplasm. Azure B, pH 4.1 for RNA. 13. Mature sperm from an adult male of lycosid spider to show the distribution of DNA in the helically coiled, densely stained, hollow rings or bar profiles seen in paraffin sections of spider testis. The crescent-shaped sperm nuclei are coiled in a head to tail fashion to form a nuclear band or bracelet that is thicker in its mid region, thinner at its tips and show a hollow center when viewed face on. Feulgen reaction for DNA. 14. Loss of staining for basic nucleoproteins by mature sperm in an adjacent section of testis from the same male of lycosid spider following extraction of DNA by 5% trichloroacetic acid at 90 °C and staining for histone proteins with fast green at pH 8.1. See text for additional details. 15. Retention of arginine-rich proteins by mature sperm in an adjacent section of testis from the same male of lycosid spider following extraction of DNA by 5% trichloroacetic acid at 90 °C and staining with the Sakaguchi reaction for arginine. 16. Glycoprotein sheaths enclosing individual mature sperm from a male of lycosid spider after staining with the periodic acid Schiff reaction for polysaccharides.

and thinner at its tips. This unique configuration was described in detail by Millot (1949, fig. 456), which shows a helically coiled nucleus that accounts for the appearance of a compacted ring of DNA encircling a hollow center in face-on views of flattened sperm. It also explains the darker, but much thinner profiles seen in views from the topside (or underside) of the coiled bracelets formed by chromatin condensation during sperm maturation. The sperm shown in Fig. 13 were stained with the Feulgen reaction for DNA to illustrate aspects of the flattened coil vs. the vertical coil which is at 90° to the plane of the former. This spiral coiling of sperm nuclei in sectioned material is somewhat obscured after PAS staining, which reveals a thin glycoprotein sheath that envelopes individual sperm (Fig. 15). Reger (1970) has also described the development of a prominent acrosome and rounding up of the sperm nucleus during spermiogenesis in the spider *Pisaurina* sp.

To determine if changes in the histone proteins associated with DNA occur during sperm maturation in spiders, the alkaline fast green technique introduced by Alfert & Geschwind (1953) was applied to slides carrying sections of the same male described above. Chicken and trout blood films and sections of trout and cat testis were processed simultaneously with sections of the spider tissues. In all cases, treatment for 15 min with just with distilled water at 90 °C prior to staining in alkaline fast green showed no staining of either somatic or sperm nuclei. Pretreatment with 5% TCA at 90 °C to extract DNA, followed by staining in fast green at pH 8.1 resulted in coloration only in nuclei of the book lung and other somatic tissues adjacent to the testis, but the sperm remained unstained (Table 1, Fig. 14). These sperm "ghosts," recognized by their unique morphology and hollow centers, were readily visualized in the sections by phase microscopy and were well stained in a replicate preparation of sections from the same testis using the cytochemical reaction for arginine (Table 1, Fig. 15). As expected, blood cell nuclei of chicken and trout were well stained by alkaline fast green after acid extraction of DNA, but the sperm of trout and cat also remained unstained by alkaline fast green after the hot 5% TCA treatment. Both showed substantial concentrations of arginine reaction product in companion preparations (Table 1). Each of the tissues tested for histone staining was matched by a slide stained with the Feulgen reaction for DNA to demonstrate the stability of the nuclear basic proteins of sperm to hydrolysis in 5 N HCl (Table 1). The absence of fast green staining in sperm after DNA extraction by TCA and their retention of a high concentration of arginine reaction products suggests that a conversion from a primarily histone type of basic nucleoprotein to a more arginine-rich, protamine-like protein accompanies spermiogenesis in these spiders.

Glycoprotein staining.—Periodic acid hydrolysis followed by localization of reactive aldehyde groups with the Schiff reagent results in extensive staining in sections of spider tissues fixed in MFA. In addition to staining of the coating of individual sperm (Fig. 16) accumulation of reaction product is prominent in the zymogen granules of gut diverticula, the ducts of silk glands and the walls of the air pockets in the book lung (Fig. 9). Densely stained PAS-positive droplets and globules are characteristic of the secretory tissues of gut diverticula and appear similar in size and location to the azurophilic droplets and granules described earlier. Presumably, these deposits reflect the presence of acid hydrolases secreted by digestive tissues Control slides with sections cut from the same tissue block and treated only with distilled water before staining with the Schiff reagent remain unstained. Additional studies with histochemical reactions for lysosomal enzymes and more selective digestion of substrates with other aldehyde producing reagents are needed to characterize the large concentrations of glycoproteins seen in spider tissues. Pretreatment of sections with diastase did not produce detectable differences in the intensity of Schiff staining for glycol groups when compared with control slides.

DISCUSSION

The cytochemical observations chronicled here are just the beginning of more detailed studies to explore the large variety of cell types with very specific functions and developmental histories available among arachnids and other arthropods, such as centipedes, millipedes, mites or ticks. These studies complement our cytophotometric analysis of endonuclear DNA replication in lycosid spiders (Rasch & Connelly 2004).

The wide diversity of types of cells and staining properties of spider tissues is particularly well demonstrated by the intense basophilia with Azure B due to high concentrations of RNA in the large secretory cells of the mid gut epithelium (Figs. 3–4) and in the nucleoli and cytoplasm of immature oocytes (Figs. 10–12). The latter finding confirms an early study by Edström (1960) based on his analysis of ultraviolet absorption curves to assess levels of RNA in the nucleoli and cytoplasm of oocytes of the common house spider *Tegenaria domestica* (Clerck 1757). The synthesis and accumulation of ribosomal RNA in both organelles is to be expected for a tissue about to embark upon a course of extensive yolk deposition prior to egg maturation. Glycoprotein staining after using the PAS reaction clearly detailed many delicate deposits of chitin lining chambers of the book lung (Figs. 7–9). Our study of the histone proteins of mature sperm of lycosid spiders has demonstrated that their sperm undergo conversion to an arginine-rich, protamine-like protein during spermiogensis (Figs. 13–15), similar to the pattern of changes found for the sperm of trout and several other animal species (Alfert 1956). We also found that there is a thin glycoprotein sheath enclosing individual sperm (Fig. 16). The special fixation protocols and tissue maceration techniques used by Chen (1999) in his elegant analysis of chromosomes for 6 species of spiders from Taiwan were not employed in the present study and therefore preclude useful comparisons with his findings. No mitotic figures were observed in any of the tissues examined here.

As shown by previous cytochemical studies of silk glands in *Antrodiaetus* which is very distantly related to lycosids (Palmer et al. 1982) and *Euagrus* (Palmer 1985), cells of these organs are morphologically and functionally diverse. These and many other species of spiders with special cellular adaptations in poison glands, silk producing glands and other tissues that produce a variety of proteins (Palmer et al. 1982; Palmer 1985; Foelix 1996; Felgenhauer 1999; Vollrath & Knight 2001) provide a broad landscape for future research of potential cell models from a group of understudied arthropods with a long history on earth.

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ANAEROBIC METABOLISM AND MAXIMAL RUNNING IN THE SCORPION *CENTRUROIDES HENTZI* (BANKS) (SCORPIONES, BUTHIDAE)

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ABSTRACT. When forced by prodding to run continuously, *Centruroides hentzi* (Banks 1901) (Scorpiones, Buthidae) lost over 70% of initial speed within 30 s and moved fitfully, if at all, after 90 s. A lack of behavioral response to alternative stimuli presented after two mins of prodding suggested that the scorpions were physiologically fatigued. Mean whole body D-(-)-lactate concentration increased from resting values of 0.6 μmol/g to 4 μmol/g at exhaustion, an approximately 6.5-fold change. It is unlikely that scorpions accumulate significant amounts of other anaerobic products. Whole body lactate accumulations in *C. hentzi* are lower than those found in species of spiders, crabs and terrestrial ectothermic vertebrates that are more specialized for running. This difference may be the result of proportionately more non-locomotory body mass in the bodies of scorpions compared to these other animals and not due to lower rates of anaerobic metabolism within locomotory muscles.

Keywords: D-(-)-lactate, running, exercise

Scorpions have low resting rates of aerobic metabolism; typically only 25% of many other terrestrial arthropods (Anderson 1970; Lighton et al. 2001). This, combined with a low-activity sit-and-wait or slow search predatory style, means that total energy expenditures are small. The result is that scorpions are able to endure periods of low food availability and to convert a large portion of their food into biomass or progeny (Lighton et al. 2001). In some arid ecosystems scorpion biomass may exceed that of all vertebrates combined (Polis & Yamashita 1991).

For any animal to engage in vigorous activities such as prey capture or predator avoidance, it must be able to provide ATP at rates that match the demands of active muscles. Good, albeit limited, evidence from vertebrates suggests that animals with low resting rates of aerobic metabolism also have low maximum rates of aerobic metabolism (Rezende et al. 2004). Moreover, in burst activity there is little time to fully activate the subcellular and organ system components of aerobic metabolism. In most groups of animals, sudden onset, high power requirements are largely met by anaerobic glycolysis and the depletion of high-energy phosphate storage compounds such as arginine phosphate or creatine phosphate (McArdle et al. 2001). Within

the arachnids, the importance of these pathways is well documented in spiders (Prestwich 1983a, b, 1988a, b). Scorpions possess respiratory and circulatory structures that are similar to those of spiders, and, like many spiders, they are not highly active predators. Given these similarities and their low resting rates of metabolism, it is reasonable to expect that scorpions would also rely on anaerobic metabolism during intense activity.

The only previous data on anaerobic metabolism in scorpions was the finding by Long & Kaplan (1968) that *Centruroides sculpturatus* Ewing (1928), possessed a high activity of the enzyme D-(-)-lactate dehydrogenase (dLDH). This same enzyme is found in high activity in spiders (Long & Kaplan 1968; Prestwich & Ing 1982) where it is associated with production of D-(-)-lactate at rates that depend on the species and intensity of activity; measurable accumulations may be found after 5 to 10 s of intense running or struggle (Prestwich 1983a,b, 1988a,b). The work presented in this paper confirms that at least one species of scorpion also produces substantial amounts of D-lactate during forced running.

METHODS

Animals.—*Centruroides hentzi* (Banks 1901), also referred to as Hentz's striped bark

scorpion, is a small scorpion whose geographic range is essentially restricted to Florida (Shelley & Sissom 1995). It has a low resting rate of metabolism (Anderson 1970). I collected adults from under the bark of dead trees in pasture parklands and woods located within 15 km of location 29.671° N, 82.458° W (northwest of Gainesville, Alachua County, Florida). Since all individuals were used destructively (see below), there are no voucher specimens. I housed the scorpions individually in plastic cages containing dry sand, pine bark, and a water source at 25 °C on a 12L: 12D schedule and fed them early instar crickets every four days. The last feeding was five days prior to their use in an experiment so as to put all in a comparable nutritional state (Anderson 1974).

Forced Running Performance.—I forced all individuals to run in a rectangular arena measuring 1.0 (L) × 0.3 (W) × 0.2 (H) meters that had an interior marked in 0.1 m grids. I stimulated running by touching their telsons with a blunt rod. I determined running speeds by measuring the distance run over 5 s and dividing by time to obtain speed in m/s. I divided this result by the body length. All exercise took place at 25 °C.

To be sure that what appeared to be fatigue was not merely habituation to prodding, I exercised five individuals by prodding them until they moved only very slowly and then brought a hot soldering iron near them (they were not touched). In rested individuals this heat stimulus always produced rapid running.

Anaerobic Metabolism.—The day after the running speed measurements, all individuals were used destructively to obtain lactate samples in one of four separate treatment groups: two rest groups and two exercise groups. There were no statistically significant differences in the masses of the individuals in each group (one-way ANOVA, $P = 0.28$, 16, 3 df). I observed the resting individuals for about one hour to be sure that they did not struggle or make more than minor, isolated movements. I then froze them by immersion in liquid N_2. I ran the exercise groups in the arena as described above for two mins and then also froze these individuals in liquid N_2.

I homogenized the frozen members of one rest and exercise group in ice-cold 10% tricholoroacetic acid (TCA) and the remaining rest and exercise groups in ice-cold 0.6 M

$HClO_4$. The difference in procedure is necessitated by the two different methods of analysis I used for lactate; TCA was not consistent with the enzymatic techniques and $HClO_4$ was not consistent with the colorimetric technique. Protein precipitants from these acid treatments were removed by filtration (Prestwich 1983a).

I analyzed the deproteiniated filtrates of $HClO_4$-treated rest and exhaustion samples enzymatically for both D- and L-lactate using the method of Gawehn & Bergmeyer (1974). To do this, I performed the assay the same way except that in one case I used the D-optical isomer specific enzyme and in the other I used the L- specific form. Assays of each type were in duplicate with a total buffer and reactant volume of 0.8 ml. All biochemicals and buffer constituents used in these assays were purchased from Sigma Biochemicals, St. Louis, Missouri, USA (now Sigma-Aldrich) and were the highest purity available.

I analyzed the other rest and exercise groups (those homogenized in TCA) for anaerobic products using the less specific colorimetric technique of Barker & Summerson (1941) modified for micro samples by Harrower and Brown (1972) and further modified for arachnids by Prestwich (1983a). I analyzed each animal's sample in duplicate with its own lactate-free blank (Prestwich 1983a). This method uses hot acid to generate acetaldehyde from lactic acid; the acetaldehyde then reacts with a dye to produce a color change. Certain other compounds (e.g., some glycolytic intermediates) also react under these conditions to cause color change but they tend to be at low concentration (Barker & Summerson 1941). In earlier work on spiders I found that this method typically gave resting lactate concentrations that were up to 10% higher than found enzymatically, probably as a result of its being less specific (Prestwich 1983). For the present study, I assumed that a discrepancy between colorimetric and enzymatic analysis results for exercised scorpions that approached or exceeded 10% would suggest accumulation of anaerobic by-products in addition to lactate because total amounts of these other compounds would be greater than at rest.

RESULTS

Running.—Figure 1 presents average forced running speeds in body lengths per second with respect to time at 25 °C. These small
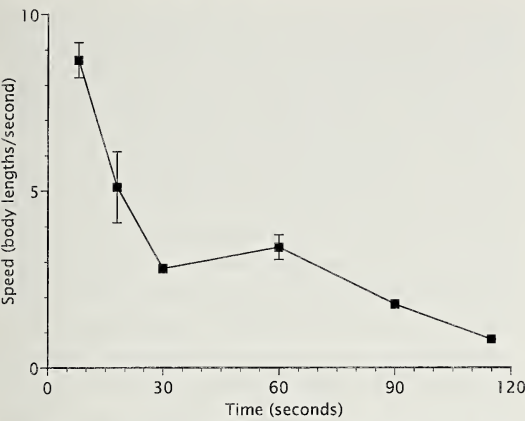
Figure 1.—Running speed in *Centruroides hentzi* during a two min forced activity bout. Speed decreases rapidly over the first 30 s. Error bars indicate 95% confidence intervals. For each point n = 14. Mean body length was 4.7 ± 0.3 cm (SE).

scorpions were surprisingly fast for the first 10 seconds and ran at speeds like those reported by Shaffer & Formanowicz (1996) for a similarly sized species, *C. vittatus* (Say 1821). However within 20 s of the start of exercise, *C. hentzi*'s speed decreased by over 50%; after 30 s, the speed was reduced by nearly 70%. Thereafter, speed reductions were more gradual and some individuals only moved when prodded continuously. Application of the alternative (heat) stimulus (see Methods) at either 30 or 120 s produced no change in activity. This implied that fatigue observed at those times was not the result of habituation to the prod.

Lactate metabolism.—Table 1 presents the results of the different assays for anaerobic products. The non-specific assay (column 1) shows that a small compound or compounds with chemical properties similar or identical to lactic acid is/are present at rest and then accumulate(s) during two mins of forced activity. The compound is not the L(+) optical isomer of lactate (the one found in many animals, including perhaps all chordates). I detected none in two different groups of scorpions that were either resting or exercised for two minutes. When I analyzed these same samples for the D(-) optical isomer, I found this substance in resting scorpions at levels that are statistically indistinguishable from the results of the non-specific test. At the completion of two mins of forced exercise, D(-)-lactate concentration had increased significantly to values about 5.8 times those at rest. The total accumulation of lactate or lactate-mimicking compound(s) in the colorimetric test was about 7% greater than the value found for D-lactate, a statistically significantly difference (ANOVA, $P = 0.03$, 1,8 df) similar to that observed in spiders (Prestwich 1983a).

DISCUSSION

Rapid fatigue during forced running by *C. hentzi* (Fig. 1) is not expected in aerobically fueled activity. In spiders, a similar pattern is associated with accumulation of anaerobic by-products and depletion of arginine phosphate (Prestwich 1983a, b, 1988b). Although there are undercurrents of controversy in the exercise science community, the consensus continues to be that lactate accumulation is associated with fatigue because cells are not fully able to buffer H^+ ions that accumulate when lactate is produced but not sufficiently eliminated (McArdle et al. 2001). This must be especially true in animals that possess limited aerobic capacities and lack highly efficient circulatory mechanisms to move lactate away from muscles to other parts of the body.

Table 1.—Estimates of anaerobic metabolism in the scorpion *Centruroides hentzi*. Sample sizes refer to each treatment. Mean mass and S.E. for each treatment group is given in parentheses.

Condition of scorpion	Anaerobic Products (μmol/g, $\overline{X}$ ± SEM)		
	Colorimetric assay (Non-specific) $n = 6$	D-($-$)-lactate $n = 4$	L-($+$)-lactate $n = 4$
Rest	0.59 ± 0.003 (0.192 ± 0.010 g)	0.67 ± 0.15 (0.178 ± 0.021 g)	None detected
Two min forced activity	4.15 ± 0.044 (0.181 ± 0.007 g)	3.91 ± 0.07 (0.185 ± 0.015 g)	None detected
Change	3.56	3.34	—

Anaerobic products such as D-lactate are best viewed not as wastes, but instead as storage molecules consisting of an energy-rich carbon skeleton (pyruvate in this case) to which has been added a pair of energy-carrying electrons. These electrons were removed from an earlier glycolytic intermediate. Under conditions where a muscle cell has sufficient aerobic capacity they would instead have been shuttled to the mitochondria to provide an energy source to synthesize ATP. This process can be reversed; lactate can by fully oxidized at a time or place in the scorpion where aerobic conditions exist.

A number of other compounds (e.g., alanine or glycerol-3-phosphate) may potentially serve the same purpose (Prestwich & Ing 1982; Prestwich 1983a). Small accumulations of such compounds could possibly account for the slightly greater concentrations of "lactate-like" molecules reported by the colorimetric method as compared to the enzymatic assay (Table 1). However, this difference is small (7%) and could just as well have been due to slight differences in the performances of the individuals that make up the two exercise treatment groups. It is reasonable to conclude that D-lactate is the major if not only anaerobic by product in C. hentzi and perhaps all scorpions.

It is unknown why chelicerates produce the D optical isomer of lactate whilst other arthropods, such as crustaceans, produce the L optical isomer and others (most insects) appear to have lost the expression of the LDH gene (Long & Kaplan 1968; Sacktor & Wormser-Shavit 1966). It is possible that the two enzymes may have significant structural differences—arthropod D-LDH has a molecular weight less than half that of L-LDH (Long & Kaplan 1968) but it is also possible that the difference is that arthropod L-LDH is a dimer and D-LDH a monomer and that differences are less than suggested by their apparent molecular weights. There is no evident functional advantage of one version of this enzyme over the other. Both readily reduce pyruvate to lactate, and thereby help to maintain a redox state that allows glycolysis to proceed.

The resting and exhaustion lactate concentrations reported in Table 1 are about half of those measured in spiders (Prestwich 1983a; Anderson & Prestwich 1985), terrestrial crabs (Full & Herreid 1984; Full 1987) and terrestrial ectothermic vertebrates (Bennett 1978). This does not mean that individual active scorpion muscles produce less lactate. The most likely explanation is that the proportion of body mass devoted to running muscles is lower in scorpions than in these comparison groups. Approximately 70% of the total body mass of C. hentzi is made up of tissues likely to have no more than minor involvement in running: the opisthosoma, telson and chelapeds. By contrast, in spiders, both leg and prosomal muscles are heavily involved in locomotion (Anderson & Prestwich 1974) and opisthosomal mass was often no more than 40% of total mass (Prestwich 1983a, b).

The extensive use of anaerobic metabolism by intensely active scorpions and spiders may be a consequence of using pressure to extend certain joints and is part of a suite of adaptations that relate to low energy expenditure. In spiders, prosomal pressures as high as 450 torr are generated during struggling, running and jumping and these prevent the circulation of well-oxygenated hemolymph from the book lungs to active muscles because maximum cardiac pressures are below 100 torr (Parry & Brown 1959; Anderson & Prestwich 1974; Prestwich 1988a, b). In scorpions, hemolymph pressures that reach 200 torr are used in conjunction with elasticity to extend certain joints lacking extensor muscles, particularly the chela (Alexander 1967; Sensenig & Shultz 2003, 2004). If hemolymph pressures are high near active muscles, it is reasonable to predict low oxygen availability and reliance on anaerobic metabolism.

Anaerobic metabolism seems to represent an "inexpensive" alternative to reliance on aerobic processes for fueling movement. Compared to the aerobic pathway proteins and cytochromes of the mitochondria, relatively few types of proteins need to be produced to support anaerobic metabolism. It must be noted that the energetic advantage of building and maintaining fewer mitochondria is lessened somewhat by the need to synthesize high concentrations of the enzymes required to achieve high rates of anaerobic metabolism. However, anaerobic systems do not require the well-developed circulatory and respiratory system supports needed by highly active cellular aerobic systems. This, in turn, helps to enable a low resting rate of metabolism—a boon to scorpions, spiders, and likely other

exclusively predaceous orders of arachnids that are adapted to irregular and low food availability (Anderson 1970, 1974; Prestwich 1983b; Lighton et al. 2001).

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A NEW SPECIES OF THOMISID SPIDER (ARANEAE, THOMISIDAE) FROM THE SOCIETY ISLANDS WITH A DESCRIPTION OF THE MALE OF *MISUMENOPS MELLOLEITAOI*

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ABSTRACT.   This study revises the status of crab spiders (Araneae, Thomisidae) endemic to the Society Islands, a volcanic archipelago situated in the southern Pacific Ocean. Only one species, *Misumenops melloleitaoi* Berland 1934, known from a single female and immature, was previously recorded from Tahiti (the largest island of the Society archipelago). Field surveys (1999–2003) and examination of material in natural history collections show that thomisid spiders occur in four islands of the Society archipelago and are recognized as two endemic species. *Misumenops temihana* is described as new from the islands of Raiatea and Huahine. This paper further presents the first description of the male of *M. melloleitaoi* Berland 1934, and extends the range of this species to include multiple localities on the islands of Tahiti and Moorea. *Misumenops melloleitaoi* can be easily distinguished from *M. temihana* by the presence of two short black lines on the ventral surface of femur and patella I and II which are lacking in *M. temihana*.

Keywords: Polynesia, spider, Tahiti, Thomisidae, taxonomy

Invertebrate faunas of remote oceanic islands are generally characterized as taxonomically depauperate at the familial and generic levels yet often harbor exceptionally high numbers of endemic species (Gressitt 1961; Gillespie & Roderick 2002). The extremes of this pattern are exemplified in the Hawaiian Islands where approximately 10% of all known spider families occur naturally, yet an extremely high proportion of native spider species (~98%) are considered endemic to the archipelago (Nishida 1997). The unique biotic composition of the Hawaiian Islands has drawn considerable attention to the importance of documenting its native invertebrate fauna in the face of increasing threats from invasive species and habitat destruction (Howarth & Mull 1992; Gillespie 1999). While it is certain that many Hawaiian species remain to be described, the archipelago's native spider fauna is undoubtedly the most thoroughly studied among all Polynesian archipelagos (Gillespie et al. 1998). In contrast, little is known of the spiders of the Society Islands,

another remote Polynesian archipelago located ~4000 km south of the Hawaiian Islands.

The Society archipelago consists of six high islands, the largest of which is Tahiti (Fig. 1). Knowledge of the Society Islands' spider fauna is fragmentary, and stems predominantly from descriptions by Berland (1934, 1942) based on the small amount of material collected during the Pacific Entomological Survey in 1928 by A.M. Adamson and the Mangarevan Expedition in 1934 by E.C. Zimmerman, both in association with the Bernice Pauahi Bishop Museum. Since then, the spider fauna of the Society Islands has received little taxonomic attention with the exception of a revision of the genus *Tetragnatha* (Gillespie 2003) in which three new endemic species were described. Given that the biota of the Society Islands, in common with that of other remote islands (Myers et al. 2000), is threatened by invasive species and habitat destruction (Meyer 2004), it is critical to document the diversity and distribution of species endemic to this archipelago.

Representatives of the family Thomisidae occur in several remote island archipelagos across the central Pacific Ocean. The majority of described thomisid species from this region

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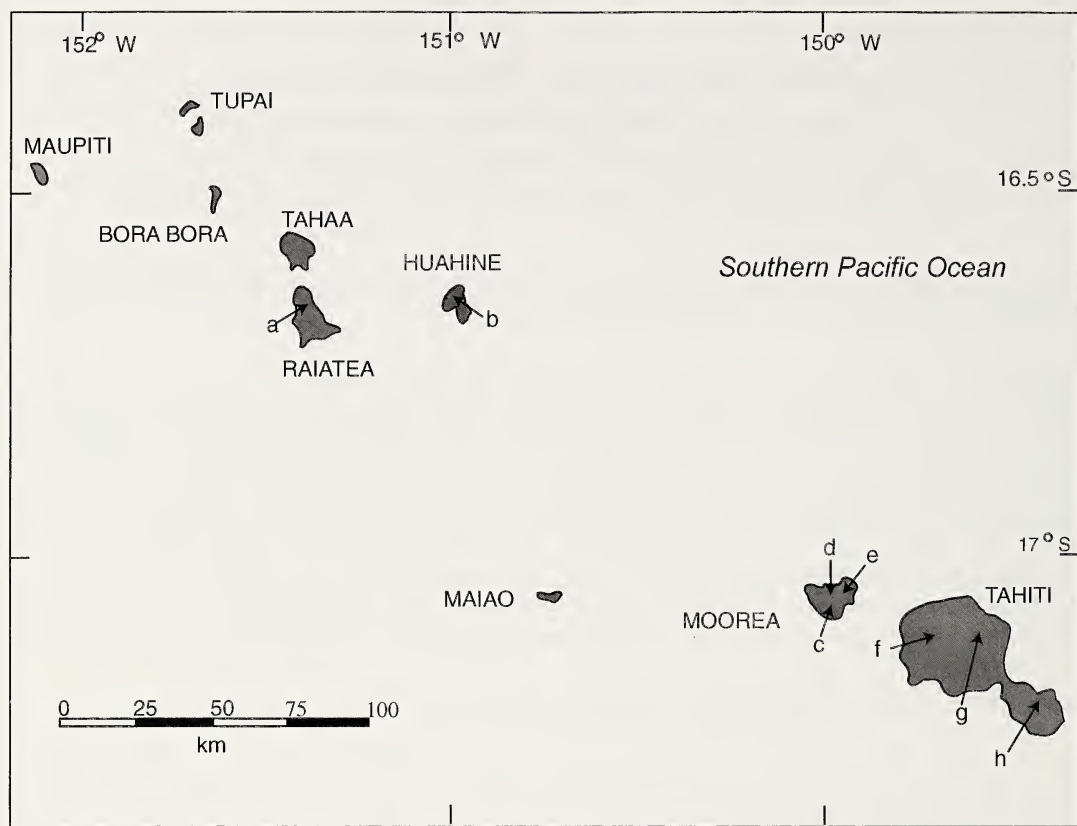
Figure 1.—Map of Society Islands archipelago, with arrows indicating localities where specimens were collected during recent expeditions (1999–2003): a = Temihana Plateau, Raiatea; b = Mt. Turi, Huahine; c = Le Belvedere Lookout Trail, Moorea; d = Mt. Mouaputa, Moorea; e = Vaire-Paopao Trail, Moorea; f = Mt. Aorai, Tahiti; g = Mt. Marau, Tahiti; h = summit, Belevedere Rd., Tahiti-Iti.

occur in the Hawaiian archipelago, with 20 endemic species, 16 of which are currently assigned to the genus *Misumenops* F.O. P.-Cambridge 1900 (Suman 1970; Platnick 2006). Species of this cosmopolitan genus also occur in three other Polynesian hot-spot archipelagos: the Marquesas, the Austral Islands and Society Islands. From each of these three archipelagos, a single, endemic *Misumenops* species is recognized representing the only known thomisid. Berland (1934) described *M. pallida* from one female and one immature specimen collected in Vaipuarii Valley, Tahiti Island in 1928. Subsequently, C.F. de Mello-Leitão notified Berland that *M. pallida* was a junior secondary homonym of *M. pallidus* (Keyserling 1880) (Berland 1942). Accordingly, Berland (1942) selected *M. melloleitaoi* as a replacement name. No further records of thomisids from the Society Islands, either native or introduced, were found in the literature

during the preparation of this manuscript (Platnick 2006).

As part of this study, Garb (2003) and Garb & Gillespie (2006) have investigated phylogenetic relationships between the Society Islands' *Misumenops* and congeners found in other Polynesian archipelagos using both mitochondrial and nuclear gene sequences, including specimens examined here. The present study revises taxonomic knowledge of the thomisid spiders from the Society Islands, in part based on specimens found during recent expeditions (years 1999–2003) on four islands (Raiatea, Huahine, Moorea and Tahiti), in addition to material housed in natural history collections.

METHODS

Descriptions were based on specimens previously collected from the Society Islands and deposited in the Bernice Pauahi Bishop Mu-

seum, Honolulu (BPBM) as well as material recently collected by the author and/or by colleagues (listed below) during several expeditions to Tahiti as well as to Moorea, Raiatea, Huahine and Bora Bora (Fig. 1). Live specimens were found in the mountainous interior of all of these islands except Bora Bora, at elevations ranging from 350–1240 m above sea level, and collected by beating vegetation onto a sheet, noting the plant species whenever possible. These specimens were initially preserved in 95% ethanol, and subsequently transferred to 75% ethanol. All specimens were visually examined using a Leica Wild M3Z Kombi stereo-microscope fitted with a camera lucida. All available adult specimens were examined in order to determine diagnostic characters as well as to assess the range of variability within a taxon. Measurements were recorded in millimeters using an eyepiece micrometer scale. Vellum illustrations were scanned into Adobe Photoshop® and saved as TIFF files.

Characters examined.—Length and width measurements were taken of the cephalothorax and abdomen from a dorsal view, with the width determined at its widest point. Length for each leg segment was measured at the dorsal margin. The distribution and arrangement of macrosetae were recorded for each leg article (legs I–IV) as well as for the cephalothorax. Eye arrangement, specifically the distances between the PME, AME, PLE and ALE were measured. Male pedipalps and legs of some specimens were excised (later retained in microvials with specimens) to examine at greater magnification. The shape and degree of sclerotization were examined for both the embolus and retrolateral tibial apophysis. External female genitalia were examined, including shape and size of the epigynal guide pocket, intromittent orifices, spermathecae and spermathecal apophyses. Specimen coloration and color patterning were described as observed in living and preserved specimens. The presence of thin, darkly pigmented lines, as similarly found ventrally on the femora, patella and tibia of Hawaiian *Misumenops* species (Suman 1970), was also recorded.

Terminology.—Abbreviations related to morphological terminology are as follows: retrolateral tibial apophysis (RTA); ventral tibial apophysis (VTA); anterior median eyes (AME); anterior lateral eyes (ALE); posterior median eyes (PME); posterior lateral eyes (PLE). Terminology relating to the carapace follows terms established by Schick (1965). Specimens are deposited in the Bernice Pauahi Bishop Museum (BPBM), Honolulu, and the Essig Museum of Entomology at the University of California (EMUC). The contraction JEG-### (e.g., JEG-461), indicates the code number of individual specimens from the author's collection database. Collections were made by the author (JEG), Rosemary Gillespie (RGG), George Roderick (GKR), Joseph Spagna (JS), Miquel Arnedo (MA), Steve Lew (SL), Leo Shapiro (LS), Alexa Bely (AB) or Elin Claridge (EC).

TAXONOMY

Family Thomisidae Sundevall 1833
Genus *Misumenops* F.O. P.-Cambridge 1900

Type species.—*Misumena maculisssparsus* Keyserling 1891, by original designation.

Remarks.—The genus *Misumenops* consists of 108 named species and has a nearly cosmopolitan distribution, occurring in North and South America, Europe, Asia, Africa, and across islands in the central Pacific. The genus is particularly diverse in North and South America, where approximately 70% of the described species occur.

Misumenops temihana new species
Figs. 2–9, 18

Type material.—FRENCH POLYNESIA: Society Islands: Holotype male, Raiatea Island, Temihana Plateau, 780 m, 16.78°S, 151.45°W, 13 July 2000, MA, LS, and AB, (BPBM, JEG-461). Allotype female, locality and collecting data as for holotype (BPBM, JEG-459). Paratypes: *Raiatea:* 2 ♂ (JEG-467; 472) 4 ♀ (JEG-460; 465; 470; 471), 5 immatures (JEG-462; 464; 468; 469), Temihana Plateau, 780 m, 16.78°S, 151.45°W, 13 July 2000, MA, SL, LS, and AB (EMUC); *Huahine:* 2 ♀ (JEG-700; 701), Mt. Turi, 650 m, 16.71°S, 151.02°W, August 2003, EC (EMUC).

Etymology.—The specific epithet, a noun in apposition, refers to the Temihana Plateau of Raiatea Island, the type locality of this species.

Diagnosis.—*Misumenops temihana* resembles *M. melloleitaoi* but does not possess the
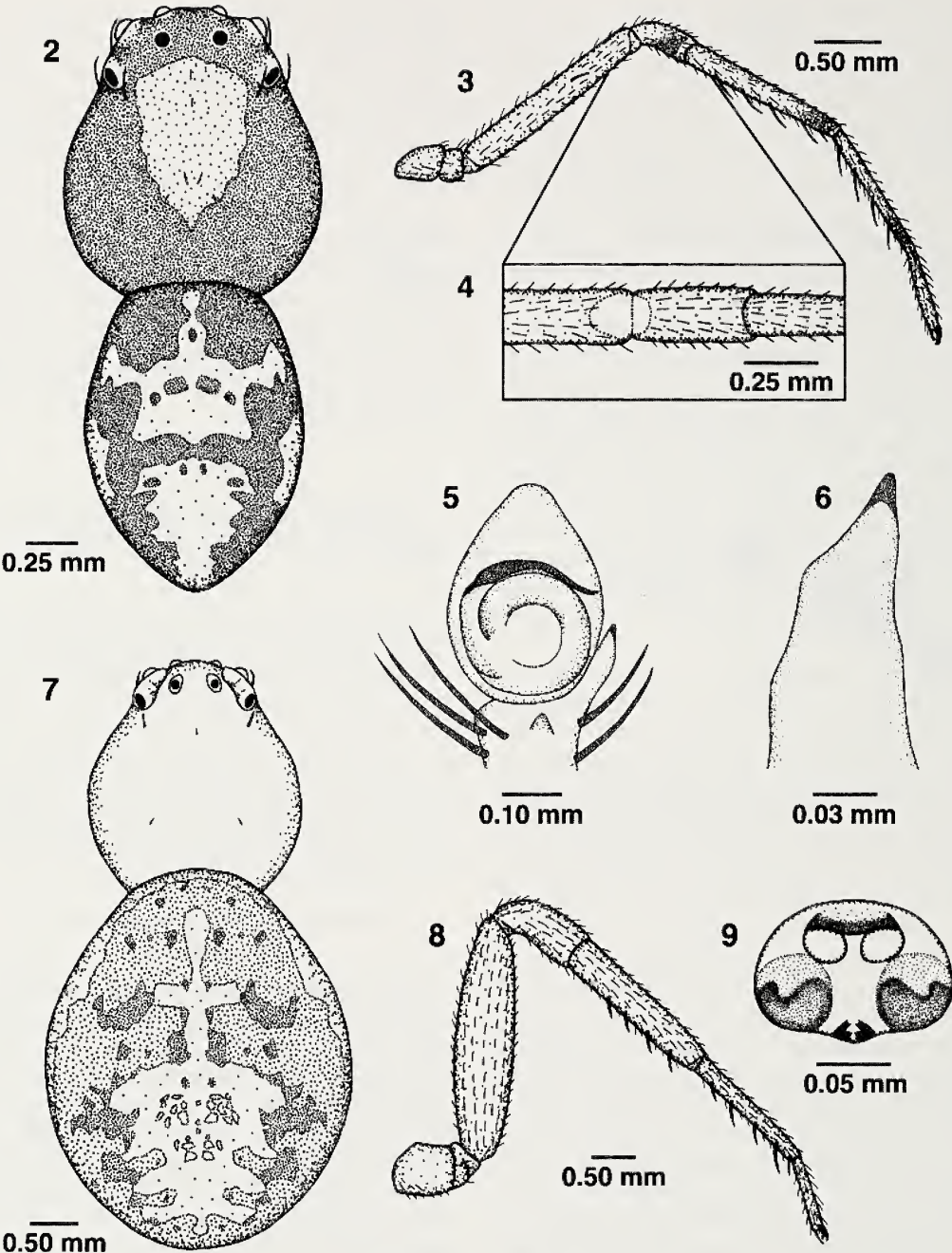
Figures 2–9.—*Misumenops temihana* new species. Male holotype (JEG-461): 2. Body, dorsal view; 3. Left leg I, prolateral surface; 4. Expanded view of ventral surface of distal portion of femur and patella I; 5. Left palp, ventral view; 6. Left tibial apophysis, retrolateral view. Female allotype (JEG-459): 7. Body, dorsal view; 8. Left leg I, prolateral surface; 9. Epigynum, ventral view.

two short black lines on the ventral surface of femur and patella I and II found in the male and female *M. melloleitaoi* (compare Figs. 4 and 12).

Description.—*Holotype male* (Figs. 2–6): Cephalothorax length 1.32; cephalothorax width 1.25; abdomen length 1.50; abdomen width 1.07. Carapace (Fig. 2) dark brown ex-
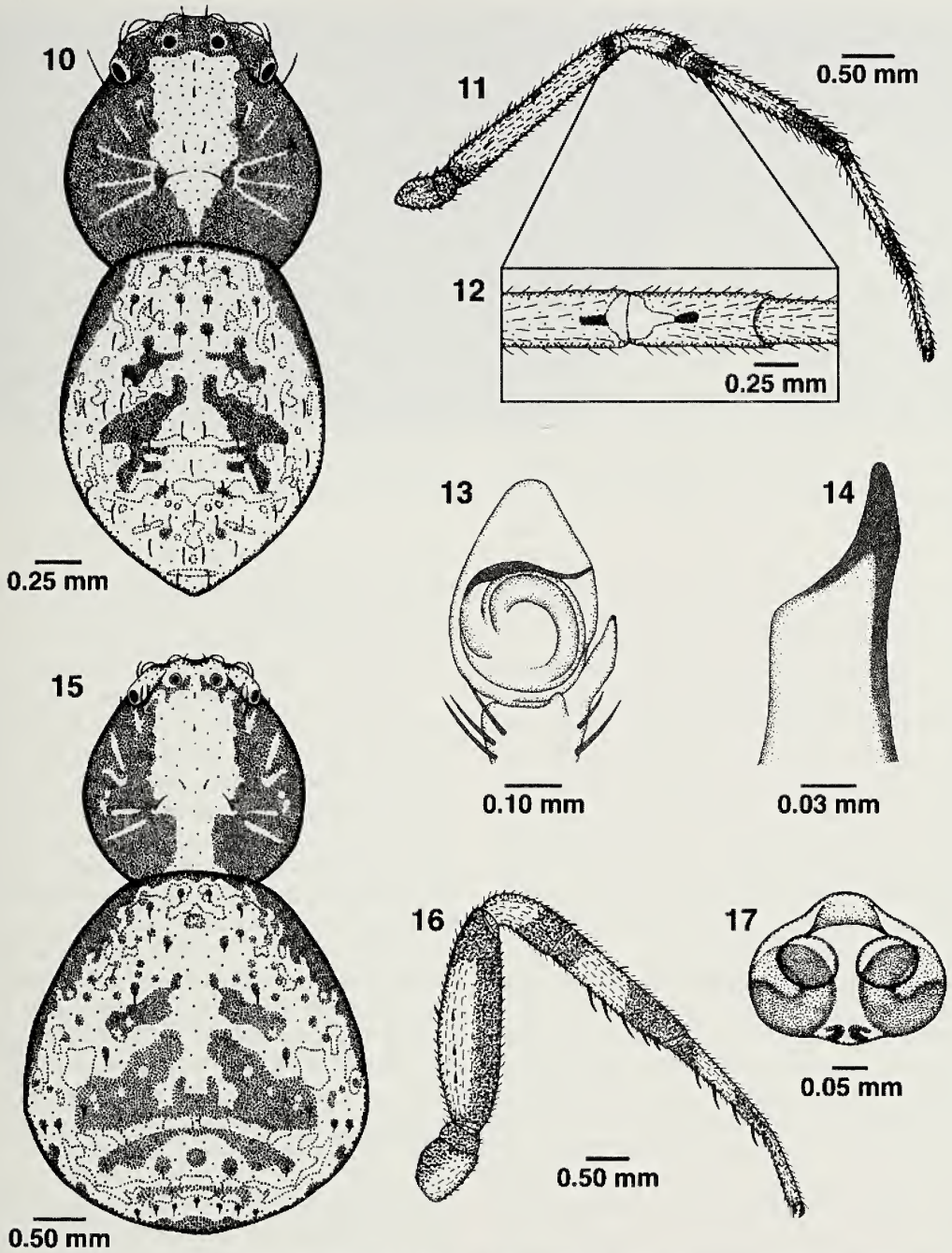
Figures 10–17.—*Misumenops melloleitaoi* Berland 193.: Male from Tahiti, collected at summit of Mt. Marau, 1240m, coll. by JEG, 6 July 2000 (JEG-449): 10. Body, dorsal view; 11. Left leg I, prolateral surface; 12. Expanded view of ventral surface of distal portion of femur and patella I; 13. Left palp, ventral view; 14. Left tibial apophysis, retrolateral view. Female (with same collecting data as male; JEG-458): 15. Body, dorsal view; 16. Left leg I, prolateral surface; 17. Epigynum, ventral view.

Figure 18.—*Misumenops temihana* new species, female allotype (JEG-459) from Temihana Plateau, Raiatea Island.   Figure 19.—*Misumenops melloleitaoi* Berland, female (JEG-484) from Mt. Mouaputa, Moorea Island.

cept for mesodiscus and metadiscus, which are yellow (yellow-green in life); sternum, labium and endites brown; distal tips of endites without pigment. Dorsum of abdomen (Fig. 2) predominately yellow with dark brown lateral bands and incomplete transverse band, "H-shaped." Venter and spinnerets uniformly light yellow with no patterning. Ocular area, clypeus and chelicerae dark brown. Eyes on yellow tubercles; ALE and PLE tubercles more pronounced; ALE and PLE approximately 2 × size of AME and PME. Distance between PME 0.21; PLE 0.71; AME 0.17; ALE 0.57. Carapace with few, short setae; prominent, long, bilaterally paired setae posterior of PLE; long setae on clypeus and chelicerae. Abdomen with sparse, short setae. Legs and pedipalps, uniformly yellow (green in life). Leg I (Fig. 3): femur 1.55; patella 0.37; tibia 1.27; metatarsus 1.11; tarsus 0.55. Leg II: femur 1.51; patella 0.58; tibia 1.44; metatarsus 1.34; tarsus 0.92. Leg III: femur 1.11; patella 0.23; tibia 1.16; metatarsus 0.66; tarsus 0.51. Leg IV: femur 1.15; patella 0.26; tibia 0.70; metatarsus 0.59; tarsus 0.49. Femur I, 1 prolateral robust macroseta; femora II–IV, each with 1 dorsal macroseta. Claw tufts sparse and simple. Palp (Fig. 5): femora with series of short setae on prolateral and ventral surfaces; 1 short macroseta on disto-dorsal margin of patellae; paired, long macrosetae on prolateral and retrolateral tibial surface. Embolus originates near prolateral margin of tegulum; embolus tip, long and narrow, slightly

curved at tip. VTA, short, undeveloped. RTA, without pronounced notches on ventral margin, slender and sclerotized at tip.

Allotype female (Figs. 7–9, 18): Female approximately 2 × length of male; cephalothorax length 2.04; cephalothorax width 2.07; abdomen length 3.70; abdomen width 3.00. Carapace (Fig. 7), including ocular area, clypeus and chelicerae uniformly yellow, without pattern (bright green in life). Sternum, labium and endites uniformly yellow (bright green in life). Dorsum of abdomen, yellow (bright yellow in life) with two wide yellow-brown longitudinal bands (red in life) meeting at anterior and posterior end of abdomen, forming an ovoid pattern; thin black crimped stripes on top of wide, brown (red in life) stripes. Sides and venter uniformly yellow. Eye tubercles bright yellow in life, ALE and PLE, approximately 2 × median eyes, ALE slightly larger than PLE. Distance between PME 0.23; PLE 1.00; AME 0.38; ALE 0.79. Distribution and morphology of setae on cephalothorax, chelicerae and abdomen similar to male. Legs and palps yellow, without stripes, bright green in life. Leg I (Fig. 8): femur 2.83; patella 0.92; tibia 1.92; metatarsus 1.50; tarsus 0.75. Leg II missing on both sides. Leg III: femur 1.59; patella 0.75; tibia 1.15; metatarsus 0.73; tarsus 0.50. Leg IV: femur 1.83; patella 0.75; tibia 1.12; metatarsus 0.81; tarsus 0.49. Femur I without macrosetae; dorsum of femora III and IV each with one macroseta. Large, robust, sclerotized macrosetae (spines) ventrally on

tibia and metatarsus. Tibia I ventrally with 4 pairs robust spines; metatarsus I ventrally with 5 pairs of spines. Claw tufts sparse, tarsal claw with large elongate distal tooth and 3 short internal teeth of equal length. Palp with paired, long macrosetae on prolateral and retrolateral tibial surface. Epigynum (Fig. 9): hood of guide pocket curves slightly towards the posterior of epigynum; intromittent orifices close together and anterior to spermathecae, width of spermatheca approximately 2 × width of intromittent orifices, spermathecal apophyses visible at posterior of epigynum as small sclerotized, opposing "comma" shapes arched towards each other.

Variation.—*Males* (*n* = 3): carapace can be mostly yellow (green in life), with two brown stripes; sternum, labium and endites can be yellow (green in life).

Females (*n* = 7): variation in color pattern on dorsum of abdomen, particularly in presence of black pigment; some females with single dorsal macroseta on femur I, females may have 4–7 pairs of robust spines ventrally on tibia I.

Natural history.—*Misumenops temihana* was collected in the montane-scrub forest of the Temihana plateau (Raiatea Island) on a diversity of native plants, adopting the thomisid habit of remaining in a stationary position upon vegetation in order to ambush prey. The bright green coloration of females of this species may provide camouflage as they await prey on foliage.

Distribution.—The present distribution of this species is restricted to the Temihana Plateau of Raiatea Island (780 m) and the summit of Mt. Turi (650 m) on Huahine Island in the Society Islands.

Misumenops melloleitaoi Berland 1942
Figs. 10–17, 19

Misumenops pallida Berland 1934:98, Figs. 1–5 [junior secondary homonym of *Misumenops pallida* (Keyserling, 1880)].

Misumenops melloleitaoi Berland 1942:6 (replacement name for *M. pallida* Berland 1934).

Material examined.—FRENCH POLYNESIA: *Tahiti*: Holotype female, 1 immature female paratype, Vaipuarii Valley, 17.66–17.75°S, 149.50–149.58°W, 1928, M. Adamson (BPBM, type #619).

Other material examined.—FRENCH POLYNESIA: *Tahiti*: 2 ♀, 1 immature, Tao-

hiri, Mt. Aorai Trail, 17.58–17.66°S, 149.47–149.50°W, 1100 m, 12 September 1934, E.C. Zimmerman (BPBM); 1 ♀, Mt. Aorai, 17.58–17.66°S, 149.47–149.50°W, 1500–1800 m, 15 September 1934, E.C. Zimmerman (BPBM); 1 ♀, Fare Rau, Ape-Aorai Trail, 17.58–17.66°S, 149.47–149.50°W, 27 April 1959, N.L.H. Krauss (BPBM); 2 immatures (JEG-510; 518), Mt. Aorai, 1700 m, 17.61°S, 149.50°W, November 1999, RGG and GKR (EMUC); 1 ♂ (JEG-356), 3 ♀ (JEG-355; 358; 359), 7 immatures (JEG-354; 357; 360–364), Tahiti Iti, Le Belvedere Rd. summit, Mt. Teatara, 650 m, 17.79°S, 149.25°W, 24 June 2000, JEG and JS (EMUC); 1 ♂ (JEG-369), 3 immatures (JEG-365; 366; 368), Tahiti Iti, Le Belvedere Rd. summit, Mt. Teatara, 650 m, 17.79°gS, 149.25°W, 7 July 2000, JEG and JS (EMUC); 4 ♂ (JEG-428; 429; 449; 457), 4 ♀ (JEG-453; 454; 456; 458), 24 immatures (JEG-427; 430–448; 450–452; 455), Mt. Marau summit, 17.61°S, 149.55°W, 1240 m, 6 July 2000, JEG, RGG, GKR, JS, MA, SL, LS, and AB (EMUC). *Moorea:* 1 ♀, 17.48–17.58°S, 149.75–149.92°W, 500–700 m, 25 September 1934, E.C. Zimmerman (BPBM); 1 ♂ (JEG-352), 2 ♀ (JEG-350; 351), 1 immature (JEG-353), Vaire-Paopao Trail summit, 325 m, 17.52°S, 149.80°W, 19 June 2000, JEG, RGG, JS, and GKR (EMUC); 3 ♂ (JEG-370; 371; 380), 1 ♀ (JEG-390), 7 immatures (JEG-372; 373; 375–378; 385), Le Belvedere Lookout Trail, 17.53–17.55°S, 149.82–149.83°W, 550 m, 27 June 2000, JEG and JS (EMUC); 1 ♂ (JEG-395), 2 ♀ (JEG-393; 396), 2 immatures (JEG-391; 392), Le Belvedere Lookout Trail, 17.53–17.55°S, 149.82–149.83°W, 550 m, 2 July 2000, coll. JEG and JS (EMUC); 1 ♂ (JEG-483), 1 ♀ (JEG-484), Mt. Mouaputa, 840 m, 17.53°S, 149.81°W, 11 July 2000, GKR, MA, SL, LS and AB (EMUC).

Diagnosis.—Male and female with short, thin black line at the distal edge of ventral surface of femora I and II, similar line at proximal edge ventrally on patellae I and II.

Description.—*Male* (Figs. 10–14): Cephalothorax length 1.28; cephalothorax width 1.13; abdomen length 1.75; abdomen width 1.31. Carapace (Fig. 10), dark brown except for mesodiscus and metadiscus which are yellow (green in life), yellow coloration continues from metadiscus towards posterior margin of carapace in the shape of an inverted trian-

gle. Sternum, labium and endites reddish-brown; anterior margin of endites and labium pale yellow. Abdomen: dorsum predominately light brown with white and black mottling, sides of abdomen dark brown; venter yellow with broad, dark longitudinal stripe posterior to epigastric furrow; region anterior to epigastric furrow and bordered by book lungs, reddish in color. Spinnerets yellow, with reddish bands. Ocular area, clypeus, and chelicerae dark brown. Distal margin of chelicerae white. Eye tubercles yellow, AME and PME approximately equivalent in size, PLE and ALE 2 × size of median eyes, with ALE slightly larger than PLE. Distance between PME 0.17; PLE 0.68; AME 0.12; ALE 0.45. Carapace, clypeus and chelicerae with few long macrosetae and numerous short setae. Abdomen covered with short, robust setae. Legs I and II yellow-brown, with wide red bands on distal margin of femur, tibia and metatarsus I and II; legs III and IV pale yellow. Ventral surface of femora I and II with short, thin black line, ~0.13 at distal edge, similar line at proximal edge ventrally on patellae I and II (Fig. 12). Leg I (Fig. 11): femur 2.07; patella 0.47; tibia 1.67; metatarsus 1.33; tarsus 0.67. Leg II: femur 2.25; patella 0.66; tibia 2.14; metatarsus 1.73; tarsus 0.89. Leg III: femur 1.13; patella 0.34; tibia 1.04; metatarsus 0.44; tarsus 0.39. Leg IV: femur 1.28; patella 0.38; tibia 1.08; metatarsus 0.42; tarsus 0.37. Femur I with 2 macrosetae on prolateral surface, 1 macroseta on dorsum; femora II–IV, each with one macroseta on dorsal surface; dorsum of tibia III with one macroseta, tibia IV with two macrosetae on dorsal surface; claw tufts sparse. Palp (Fig. 13): 1 short macroseta on disto-dorsal margin on patellae; paired, long macrosetae on prolateral and retrolateral tibial surface. Embolus similar to *M. temihana*, as well as the short undeveloped VTA. RTA similar to *M. temihana* but with narrower dorsal tip and scelerotization continuing along dorsal margin of RTA.

Female (Figs. 15–17): Cephalothorax length 2.00; cephalothorax width 2.14; abdomen length 3.45; abdomen width 3.28. Carapace (Fig. 15) dark brown laterad, center yellow (green in life). Sternum, uniformly yellow; labium and endites pale yellow-brown. Color of abdomen, and spinnerets similar to male. Eye tubercles and median ocular area yellow; clypeus and chelicerae light

brown, distal margin of chelicerae white. AME and PME approximately equal in size, PLE and ALE 2 × size of median eyes, with ALE slightly larger than PLE. Distance between PME 0.28; PLE 1.03; AME 0.24; ALE 0.76. Carapace with few, short setae; abdomen with very few short setae; clypeus and chelicerae with a few longer macrosetae. Legs I and II yellow, with thick brown bands. Short, thin black line, at distal edge ventrally on femora I and II; similar short black line on proximal edge of femora, ventrally on patellae I and II. Legs III and IV predominantly yellow, with brown stripes. Leg I (Fig. 16): femur 2.58; patella 0.91; tibia 1.75; metatarsus 1.42; tarsus 0.92. Leg II: femur 2.78; patella 1.16; tibia 1.87; metatarsus 1.55; tarsus 0.81. Leg III: femur 1.48; patella 0.52; tibia 0.93; metatarsus 0.72; tarsus 0.67. Leg IV: femur 1.41; patella 0.60; tibia 1.00; metatarsus 0.71; tarsus 0.64. Femur I with 2 prolateral, and 1 dorsal macrosetae, 1 macroseta on dorsal surface of II–IV. Tibia I and metatarsus I ventrally bearing 5 pairs of robust spines. Claw tuft sparse, tarsal comb with elongate distal tooth and 3 short equal length internal teeth. Epigynum (Fig.17): hood of guide pocket arched anteriorly; intromittent orifices wider apart than in *M. temihana*, more than half of width of spermathecae, spermathecal apophyses visible posteriad of epigynum as small sclerotized, opposing "comma" shapes, but arched away from each other.

Variation.—*Male* ($n = 13$): Color variable, sternum may be yellow and sometimes outlined in a reddish coloration; venter sometimes with less pigmentation, without coloration around spinnerets; red bands on legs I and II may be less pronounced and absent on femora; chelicerae in one individual uniformly yellow.

Female ($n = 15$): Considerable color variation, in life ranging from almost entirely yellowish-brown to individuals with a bright green cephalothorax and yellowish abdomen. Some individuals with carapace stripes of varying widths, some without stripes. Leg bands prominent in some individuals, absent in others, others with legs I and II nearly all brown; some with reddish bands around spinnerets, most without; venter frequently uniformly yellow. Femur I sometimes with 2–3 prolateral macrosetae and 1–2 dorsal macrosetae.

Natural History.—Primarily found on native plants such as *Metrosideros* spp. *Cyathea* spp., and *Dicranopteris* sp., but also on the non-native mape, *Inocarpus fagifer* (Parkinson) Fosberg.

Distribution.—This species is distributed across the islands of Moorea and Tahiti, but appears to be restricted to montane, forested areas and is found in greater abundance at higher elevations.

Remarks.—Material in the BPBM collected by E.C. Zimmerman included one vial containing 2 females and 1 immature labeled as "Taohiri, Mt. Aorai Trail, Tahiti, Society Ils. IX-12–34, 3500 ft.;" and containing a second label written with the following: "*Misumenops tahitiensis* Berland (nom nov. pour *M. pallida* Berland 1934, preoccup.)." This label suggests that Berland may have considered *M. tahitiensis* as a replacement name for *M. pallida* before selecting *M. melloleitaoi*. No records of *M. tahitiensis* were found in Platnick (2006).

DISCUSSION

This study extends the known range of thomisid spiders within the Society Islands (previously recorded from a single locality in Tahiti) by providing the first records of thomisids for the islands of Raiatea, Huahine and Moorea (Fig. 1). From the recently collected material and Bishop Museum collections, two endemic species are recognized in the Society Islands: *Misumenops melloleitaoi* and *M. temihana*. The range of the previously described *M. melloleitaoi* is expanded to include additional localities across Tahiti and the island of Moorea. This species is revised here to include the first description of the male. A newly described second species, *M. temihana*, is restricted to the islands of Raiatea and Huahine. The two species are most easily and consistently diagnosed by the presence of a short, thin black line on the ventral surface of femur and patella I and II of *M. melloleitaoi* (males and females) that are absent in *M. temihana*.

The overall somatic and genitalic morphology of *M. melloleitaoi* and *M. temihana* is similar. However, the two species exhibit considerable color variation, particularly the females of *M. melloleitaoi*, which can range from yellow-brown to bright green. The substantial color variability observed in *M. mel-*

loleitaoi may reflect an ecological adaptation to local conditions that differs among populations. Relatively slow color change has been documented in studies of certain thomisid species (Oxford & Gillespie 1998; Chittka 2001; Heiling et al. 2003), with individuals demonstrating a chameleon-like ability to resemble their surroundings through color mimicry. Accordingly, a plastic response by individuals to environmental cues is an alternative explanation of the color variation.

Misumenops melloleitaoi and *M. temihana* appear to be in greatest abundance in high elevation habitats that contain native plant species. For example, *M. melloleitaoi* was primarily collected from high elevation montane forests (550–1240 m), on native plants such as *Metrosideros* spp. *Cyathea* spp., and *Dicranopteris*. It was also found at lower elevations in Moorea (~350 m) on the non-native Tahitian chestnut, *Inocarpus fagifer*, but appeared far more abundant at the higher elevation localities, particularly at 1240 m on Mt. Marau, Tahiti. *Misumenops temihana* was found in one of the remaining tracts of native forest on Raiatea, the Temihana Plateau (780 m), an unusual scrub-montane forest dominated by native hala (*Pandanus tectorum*). *Misumenops temihana* was also found on the summit of Huahine Island, Mt. Turi (650 m). It is difficult to draw conclusions regarding the past distributions of the Society Islands' thomisids because historical records are virtually non-existent for these spiders. However, because these spiders are presently found in association with native habitats at high elevations, their distribution suggests that they may have been more widespread prior to the conversion of lower elevation native forests for agriculture, initially for the cultivation of taro.

Investigation of phylogenetic relationships between *M. melloleitaoi* and *M. temihana* as well as to other Polynesian *Misumenops*, based on mitochondrial and nuclear DNA sequences, indicated that the two Society Island species are closely related to each other but also are genetically quite distinct (Garb 2003). This result suggests that *M. melloleitaoi* and *M. temihana* are sister species that likely diverged in association with the formation of new islands that provided geographic isolation. Garb (2003) and Garb & Gillespie (2006) also found that the Society

Island taxa are most closely related to *Misumenops* species found in the Marquesan and Hawaiian Islands as well as to North American *Misumenops* species. Though the Marquesan *Misumenops delmasi* Berland 1927 most closely resembles the Society Islands' *Misumenops*, phylogenetic analyses using mitochondrial DNA did not unite the Society and Marquesan species as monophyletic (Garb & Gillepsie 2006). However, analyses of nuclear DNA sequences did support a sister group relationship between *M. delmasi* and the Society Islands' *Misumenops* (Garb 2003). In contrast, the Society Islands' *Misumenops* are much more distantly related to *M. rapaensis* Berland 1934, which is the only representative of the family occurring in the geographically closer Austral archipelago (Garb & Gillepsie 2006). These results agree well with the conclusions of Lehtinen (1993), who hypothesized the close affinities between the Society, Marquesan, Hawaiian, and North and South American *Misumenops*. Nevertheless, relationships among these groups remain somewhat uncertain and will require further examination of the nearly cosmopolitan genus *Misumenops*.

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SEXUAL DIMORPHISM IN THE METABOLIC RATE OF TWO SPECIES OF WOLF SPIDER (ARANEAE, LYCOSIDAE)

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ABSTRACT.   Spiders have long been noted as classic examples of extreme sexual dimorphism and adaptations to the lifestyle of a sit-and-wait predator. We examined sex-based differences in the metabolic rate of two species of wolf spider that differ in their degree of sexual dimorphism and predatory strategy. *Pardosa milvina* (Hentz 1877) is a small active wolf spider that does not exhibit a large degree of sexual dimorphism in body size. *Hogna helluo* (Walckenaer 1837) is a large, strongly sexually dimorphic wolf spider with large, sedentary females and smaller, active males. We found that *P. milvina* had a higher mass-specific metabolic rate than *H. helluo*. Also, *P. milvina* males had a higher metabolic rate than *P. milvina* females but there was no difference in mass-specific metabolic rate between *H. helluo* males and females. Our data demonstrate that an actively foraging species, *P. milvina*, exhibits a higher metabolic rate than species with a sit-and-wait strategy, *H. helluo*. This suggests that activity levels may be correlated with metabolic rates. In addition, we hypothesize that sexual selection and selection for specific reproductive roles may have resulted in species differences in sexual dimorphism for metabolic rate.

Keywords: Wolf spider, *Pardosa milvina*, *Hogna helluo*, sexual selection, predation

The low metabolic rate of spiders and other arachnids has been suggested as an adaptation to living in environments with unpredictable food supplies (Anderson 1970; Greenstone & Bennett 1980; Anderson & Prestwich 1982; Lighton & Fielden 1995). Among the arachnids, ticks and scorpions appear to have very low metabolic rates compared to other arthropods (Lighton & Fielden 1995; Lighton et al. 2001). Ticks are ectoparasites that rarely encounter food and spend little time actually on their hosts. Thus a low metabolic rate is likely an adaptation to the extreme sit-and-wait strategy employed by ticks (Lighton & Fielden 1995). In scorpions, it has been suggested that their low metabolic rate is due to the cannibalistic life-style of some species (Lighton et al. 2001). In addition, variation among groups of spiders suggests a similar pattern (Anderson & Prestwich 1982; Anderson 1994, 1996).

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Therefore, it appears that life-style is in some way associated with metabolic rate.

Male and female spiders exhibit quite different behaviors that are likely the result of different selective pressures acting on each sex (e.g., Walker & Rypstra 2001, 2002). For example, there is likely strong selection on females to maximize their energy intake whereas male spiders should maximize their encounter rate with females. This results in female spiders being more aggressive towards prey and having larger chelicerae and fangs to subdue prey than males (Walker & Rypstra 2002). Numerous studies have examined metabolic rates in spiders (see references above) or sexual dimorphism (e.g., Vollrath & Parker 1992; Prenter et al. 1999; Moya-Laraño et al. 2002; Walker & Rypstra 2003), but few have examined sex differences in the metabolic rate of spiders (e.g., Kotiaho 1998). The studies that have examined sex differences in basal metabolic rate have come to different conclusions regarding which sex has a higher metabolic rate. For instance Kotiaho (1998) found that female *Hygrolycosa rubrofasciata* (Ohlert 1865) have a higher metabolic rate than males. However, in *Linyphia litigiosa* (Keyserling 1886) and in *Pardosa astrigera* (L.

Koch 1878) males have higher metabolic rates than females (Tanaka & Itô 1982; Watson & Lighton 1994). These differences may be due to differences in when the animals were tested (e.g., before or after copulation) or may reflect species-specific sex differences in the metabolic rate of males and females.

Hogna helluo (Walckenaer 1837) and *Pardosa milvina* (Hentz 1877) are two species that co-occur in many different habitats across the Eastern United States (Dondale & Redner 1990). *Hogna helluo* females construct retreats while males do not. In addition, *H. helluo* are larger and more sexually dimorphic in size and activity compared to *Pardosa milvina* (Walker et al. 1999a; Walker & Rypstra 2002, 2003). *Pardosa milvina*, on the other hand, does not exhibit as large a degree of sexual size dimorphism, males and females are similar in their activity, and females do not construct retreats. One other interesting difference between *H. helluo* and *P. milvina* is that females respond differently to food deprivation (Walker et al. 1999a, b). Activity levels in *H. helluo* increase with food deprivation and only well fed females are likely to build retreats (Walker et al. 1999a, b). However, activity levels of *P. milvina* are not influenced by feeding regime (Walker et al. 1999b). This observation led us to hypothesize that *P. milvina* will have a higher resting metabolic rate than *H. helluo*. Here we test this hypothesis and determine the degree of sexual dimorphism in resting metabolic rate for *H. helluo* and *P. milvina*. Since interspecific differences in metabolic rate correlate with life–style, we predict that male *H. helluo* will have higher rates of metabolism than female *H. helluo* and that male and female *P. milvina* will have similar metabolic rates because of their similarity in activity.

METHODS

Hogna helluo and *Pardosa milvina* were field collected as sub-adults from the Ecology Research Center (Butler County, Ohio, USA at 39.5°N and 84.7°W) in the fall of 1998. Spiders were maintained in plastic soufflé cups (100 mL for *Pardosa*, 300 mL for *Hogna*) with 1–3 cm of peat moss for substrate and were held at 25 °C, 60–70% relative humidity on a 14 Light:10 Dark light cycle until they reached sexual maturity (see Walker et al. 1999a). Spiders were generally between two and three weeks post adult molt when tested. Spiders were fed to satiation one week prior to measurement of metabolic rate and none of the spiders used in this experiment had mated. All spiders were weighed before and after respirometry. Weight loss was typically 1.8% of the initial mass. The initial weight was used in calculations of metabolic rate. Spiders were given 4 h to acclimate to 20 °C before metabolic rate was measured. We utilized 20 °C as opposed to 25 °C because of the upper limit on the water bath used to maintain a constant temperature of the air flowing through the respirometer. Voucher specimens of both species are available from the Hefner Zoology Museum at Miami University.

We measured metabolic rate using a TR-3 respirometry system (Sable Systems Inc.). This system includes both a carbon dioxide (LiCor 6252) and oxygen analyzer (FC-1B) and signal conditioners to reduce electrical noise. A multiplexor interfaced to DATACAN data acquisition/analysis software (Sable Systems Inc.) allowed switching between eight individual respirometry chambers. Metabolic rates were measured using closed-system respirometry using outdoor air. The chamber was initially purged with air free of water vapor and carbon dioxide, the chambers were left closed for a standard 30 min period, and then the air was drawn from the chambers and through the analyzers (flow rate = 50 mL·min^{-1}). Carbon dioxide production and oxygen depletion between the initial and final sampling were estimated via integration (DATACAN software) and used to calculate metabolic rates over the time interval. Spiders were observed during the period of recording and individuals that exhibited high levels of activity (e.g., if they exhibited anything other than slow walking) were not used in the analysis.

Data are presented as means ± one standard error. Ten individuals were measured of each sex from both species. Differences between the sexes in mass, carbon dioxide accumulation or oxygen consumption in μL·h^{-1}, and mass specific metabolic rates (μL·g^{-1}·h^{-1}) were examined utilizing a two-factor ANOVA with sex and species as factors. Comparisons among means were done utilizing a Tukey-Kramer procedure (Sokal & Rohlf 1995). Utilizing mass specific metabolic rates assumes

Table 1.—Mean ± S.E. for live body mass and metabolic rate measurements made on male and female *Hogna helluo* and *Pardosa milvina*. Different letters in a column indicate significant differences between sex-species combinations based on a Tukey-Kramer multiple comparison procedure.

Sex-Species Combination	Mass (mg)	$\mu LO_2 \cdot h^{-1}$	$\mu LCO_2 \cdot h^{-1}$	$\mu LO_2 \cdot g^{-1} \cdot h^{-1}$	$\mu LCO_2 \cdot g^{-1} \cdot h^{-1}$
Male *H. helluo*	198 ± 14 A	26.4 ± 1.2 A	17.3 ± 1.0 A	183 ± 19 A	138.3 ± 10 A
Female *H. helluo*	617 ± 74 B	88.8 ± 8.0 B	63.2 ± 6.8 B	206 ± 20 A	144.3 ± 12 A
Male *P. milvina*	13.3 ± 0.5 C	7.8 ± 1.2 C	4.39 ± 0.6 A	647.4 ± 75 B	572 ± 76 B
Female *P. milvina*	21.0 ± 1.2 D	6.1 ± 0.6 C	4.28 ± 0.5 A	404 ± 43 C	289 ± 23 A

isometry which may or may not be appropriate. However, these comparisons and the means of these data are presented to allow easy comparison with earlier studies of metabolic rates. To control for differences in body size without assuming an isometric relationship between body mass and metabolic rate we utilized an ANCOVA with the base-ten log

of body mass as the covariate, sex and species as factors and the base-ten log of carbon dioxide accumulation or oxygen consumption in $\mu L \cdot h^{-1}$ as the response variable (Packard & Boardman 1988).

RESULTS

Females were significantly heavier than males in both species but the difference between males and females was much larger for *H. helluo* compared to *P. milvina* (Table 1, Sex * Species Interaction $F_{(1,36)} = 15.14$, $P < 0.001$). There were also significant differences in metabolic rate ($\mu L \cdot h^{-1}$, Table 1, CO_2 Production, Sex * Species Interaction $F_{(1,36)} = 61.6$, $P < 0.001$; O_2 consumption, Sex * Species Interaction $F_{(1,36)} = 44.9$, $P < 0.0001$) and mass-specific metabolic rate ($\mu L \cdot g^{-1} \cdot h^{-1}$) among the sex-species combinations based on a two-way ANOVA (Table 1; CO_2 Production, Sex * Species Interaction $F_{(1,36)} = 13.15$, $P = 0.009$; O_2 consumption, Sex * Species Interaction $F_{(1,36)} = 8.64$, $P = 0.0057$).

The allometric relationship between body mass and metabolic rate differed between species for both CO_2 Production and O_2 Consumption (log(mass) * Species Interaction CO_2: $F_{(1,32)} = 7.99$, $P = 0.008$; O_2: $F_{(1,32)} = 5.23$, $P = 0.029$). In particular, metabolic rate increased with body mass in *P. milvina* but was not related to body mass in *H. helluo* (Fig. 1). Because of the species differences in the relationship between body mass and metabolic rate (i.e., the slopes are different, so comparisons of intercepts would be meaningless), we compared metabolic rates between the sexes using a separate ANCOVA for each species with log mass as the covariate and sex as a factor. There were no significant interactions between sex and log(mass) for any of the four ANCOVA's ($F_{(1,16)} < 3.07$, $P > 0.09$) indicating that the allometric coefficients re-

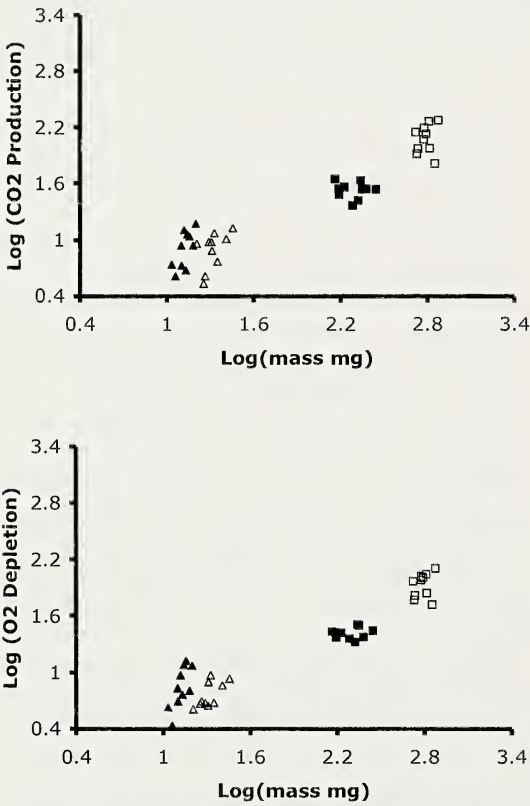Figure 1.—Relationship between log-transformed metabolic rate (CO_2 production or O_2 Consumption $\mu L \cdot h^{-1}$) and body mass for male and female *H. helluo* (squares) and *P. milvina* (triangles). Males are shown by solid symbols and females shown by open symbols.

lating metabolic rate to log transformed mass were not significantly different between the sexes. In the final analyses below, the interaction terms were not included. Given that these data span a small range of adult sizes and small sample size, estimates of the allometric coefficients may not be informative. However, it is important to note that metabolic rate increased faster with body mass in *Pardosa* compared to *Hogna* (Fig. 1). In *P. milvina*, males had a higher metabolic rate than females (Fig. 1; ANCOVA CO_2 Production, $F_{(1,17)} = 12.43$, $P = 0.0026$; O_2 consumption, $F_{(1,17)} = 8.91$, $P = 0.0083$) and in *H. helluo*, females had a higher metabolic rate than males (Fig. 1; ANCOVA CO_2 Production, $F_{(1,17)} = 5.63$, $P = 0.0297$; O_2 consumption, $F_{(1,17)} = 6.51$, $P = 0.0206$).

DISCUSSION

Hogna helluo, a typical sit-and-wait predator, had a lower metabolic rate than did *P. milvina*, a much more active species. Our data also indicate significant sexual dimorphism in metabolic rate in both *H. helluo* and *P. milvina*. Male *H. helluo* had similar mass specific metabolic rates compared to female *H. helluo*, but male *P. milvina* had higher mass specific metabolic rates than did female *P. milvina*.

Many studies have suggested associations between life-style and metabolic rate (e.g., Anderson & Prestwich 1982; Lighton & Fielden 1995). However, many of these studies examine correlations between metabolic rate and whether a group (phyla class, order or family) is presumed to be active or sedentary (Greenstone & Bennett 1980; Lighton & Fielden 1995; Lighton et al. 2001). This work has suggested that, in some cases, sit-and-wait predators do have lower metabolic rates than other comparatively sized arthropods (e.g., Lighton & Fielden 1995). However, these cases appear to be the exception not the rule. This may be due to the assumption that all species within groups are either active or sedentary when in fact they may or may not be. Our data examine differences in the metabolic rates of two species for which we have a great deal of ecological and behavioral data (Walker et al. 1999a, b; Marshall et al. 2000, 2002; Balfour et al. 2003; Buddle et al. 2003; Walker & Rypstra 2003). *Pardosa milvina* is generally more active than *H. helluo* and responds differently to periods of food deprivation sug-

gesting that the metabolic rate of *H. helluo* is lower than *P. milvina*. Our data support this hypothesis and suggest that *H. helluo* is well adapted to uncertain food supplies. It should be noted that these are only two species and our data in no way account for phylogeny (see Harvey & Pagel 1991), but these and other data (Lighton & Fielden 1995; Anderson 1996) support the hypothesis that low metabolic rates are associated with a sit-and-wait lifestyle.

Sexual dimorphism in the metabolic rate of spiders has only been documented in a few species (e.g., Kotiaho 1998). Our data and other studies indicate that sex differences in metabolic rate are not consistent across taxa. That is, in some species males have a higher metabolic rate than females whereas in others, males and females have comparable metabolic rates. In fact, our data show in *Hogna*, males and females have similar metabolic rates but in *Pardosa* males have the higher metabolic rate than females. In addition, our data suggest that these differences between the sexes in metabolic rates are not related to differences between the sexes in activity as one might predict based on the results of studies which compare active and more sedentary species. Our data are similar to results from another wolf spider, *Hygrolycosa rubrofasciata* (Kotiaho 1998) but are not consistent with sex differences in the metabolic rate in *Pardosa milvina*, *P. astrigera* and *Linyphia litigiosa* (this study; Tanaka & Itô 1982; Watson & Lighton 1994). In these studies, males have higher metabolic rates than females. Why then, is there so much variation in metabolic rate differences between the sexes across different species?

Kotiaho (1998) suggests that differences between his and Watson & Lighton's (1994) study are due to the time at which metabolic rates were measured. Watson and Lighton (1994) measured the metabolic rate of males after copulation whereas Kotiaho (1998) measured metabolic rate in males that had not copulated. This is not a factor in our study since all individuals were unmated. The second reason that Kotiaho (1998) suggests is that females in the different studies may have been in different reproductive states. That is, the metabolic rate of reproductive females is likely higher than non-reproductive females and different studies may have used females

that were not all in the same reproductive state. As adults, female *P. milvina* and *H. helluo* are adults for only one season and reproduce during the summer or early fall. Our spiders matured in the lab under conditions that mimicked the light and temperature cycle of the summer months when both species are reproductively active and thus females of both species should be in a similar reproductive state. Therefore, we feel it is unlikely that species differences in sexual dimorphism for metabolic rate can be explained by differences in the reproductive state of the females.

Sex differences in metabolism likely reflect differential selective pressures acting on males and females either due to differences in their reproductive roles and/or sexual selection. This logic has been used to explain sexual dimorphism in many different morphological and behavioral characteristics (e.g., Shine 1989; Fairbairn 1997) and could likely be used to explain sex differences in metabolism. However, we do not know enough about the physiological differences between males and females, especially the relative amounts of metabolically active tissues, to accurately predict sexual dimorphism in metabolic rate or to speculate regarding the functional and/or adaptive significance of these differences. Assuming that the sexes are created equal, we hypothesized male *H. helluo* should have a higher metabolic rate than female *H. helluo*. However, by definition males and females are different. Females have ovaries, males have testis, females accumulate more lipids than males, and it is likely that the venom glands in females are larger than those of males (Foelix 1996; Walker & Rypstra 2001). Also, do we speculate that the higher metabolic rate of male *P. milvina* is due to sexual selection (e.g., Watson & Lighton 1994) or do we suggest that female mass-specific metabolic rate is lower because of a greater proportion of metabolically inactive tissues (e.g., lipids)? Hypotheses trying to explain the nature of sex differences in metabolic rate will require integrating physiological, ecological and behavioral data.

It appears that species-specific differences in metabolic rate could be related to differences in activity. However, differences between the sexes in metabolic rate are not so easily explained. Sex differences reflect the action of differential selection pressures acting on males and females and sexual dimorphism in metabolic rate likely reflects the differential effects of sexual and natural selection on males and females and may not be due to the same mechanisms that result in species specific differences. Sexual dimorphism is a complex phenomenon that is difficult to explain and this may be particularly true of complicated physiological processes such as metabolism.

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QUANTITATIVE SHIFTS IN ORB-WEB INVESTMENT DURING DEVELOPMENT IN *NEPHILA CLAVIPES* (ARANEAE, NEPHILIDAE)

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ABSTRACT. When there are direct conflicts in resource allocation to foraging effort versus growth and development, the relative allocation to foraging may change in a predictable manner with development. Orb-webs provide a physical record of resource allocation to foraging, and their synthesis requires the investment of physiologically important resources. Spiders in strongly seasonal habitats must complete development prior to the end of the season, and may be expected to alter foraging effort to maximize the probability of successful reproduction. Comparison of populations of the orb-weaving spider *Nephila clavipes* (Araneae, Nephilidae) in very seasonal versus less seasonal habitats allows testing for changes in allocation of resources to foraging effort during development. Orb-web size increases with increasing spider size, with little variation in slope among populations. However, in univoltine populations inhabiting strongly seasonal habitats, the size of the orb web is not a simple function of spider size: the rate of increase in orb-web size decelerates abruptly at a relatively small juvenile stage. Spiders in a less seasonal habitat did not decelerate foraging investment, and the pattern cannot be explained by changes in other aspects of orb-web structure. I postulate that the decline in relative investment into foraging is related to increased investment into juvenile female growth and development in circumstances where delayed maturation carries heavy fitness penalties.

Keywords: foraging, resource allocation, juvenile development

A central premise of all foraging models is that foraging investment reflects decisions concerning the allocation of resources between obtaining food and other physiological needs (Pianka 1981; Stephens & Krebs 1986). For logistical reasons, most optimal foraging studies and models examine only one developmental stage of an organism, and they extrapolate long-term fitness consequences from short-term optimization strategies (Houston & McNamara 1982; Stephens & Krebs 1986; eg. Bilde et al. 2002). However, if the conflicts between foraging effort and other processes change during development, resource allocation decisions may vary over the life-time of an individual (reviewed in Helfman 1990).

Nephila clavipes (Linnaeus 1767) (Araneae, Nephilidae) synthesizes the viscid orb web from protein strands and other organic compounds (Townley & Tillinghast 1988; Vollrath et al. 1990), many of them physiologically important (Higgins & Rankin 1999). Individuals rebuild their orb daily or nearly daily, so resource allocation to foraging is a dynamic process (Higgins & Buskirk 1992). The orb-web is a physical representation of the investment into foraging because no foraging takes place off of the orb, and, at least in juveniles, the orb is used only for foraging. Orb-web size is a function of both the spider size and current foraging conditions (Higgins & Buskirk 1992; Sherman 1994; Pasquet et al. 1994; Higgins et al. 2001; Venner et al. 2000). However, current foraging success may not be the sole factor influencing orb-web investment (Higgins 1990, 1995).

In arthropods expressing environmentally-induced variation in development, resource allocation decisions may significantly alter growth rates and development. Many studies with diverse organisms have shown that foraging success can influence growth of juveniles and reproduction of adults (e.g., minnows, Siems & Sikes 1998; scrub jays, Fleischer et al. 2003). Fewer studies have considered the influence of development upon allocation of resources to foraging effort (apart from size-dependent factors such as changes in prey type or predation risk; however, see Cohen & Voet 2002). Habitat seasonality and individual growth and development have major effects on the fitness of individual *N. cla-*

vipes females. Female fecundity increases significantly with increasing female size (Higgins 2000). In univoltine populations, early maturing females are larger and have the opportunity to lay multiple egg sacs prior to the end of the season. Slowly growing females appear to be "making the best of a bad job" (Dawkins 1980), maturing late in the season at a small size with reduced reproductive success.

Laboratory experiments with small juvenile *N. clavipes* suggest that the spiders are making trade-offs between foraging and weight gain (Higgins 1995; Higgins & Rankin 1999). If the within-instar patterns of resource allocation are extrapolated over the entire developmental period, then when either resources or time are limiting, I predict that individual spiders will shift resources from foraging investment to growth and development, decreasing the likelihood of reproductive failure. I expect this to be most obvious in univoltine organisms inhabiting strongly seasonal areas, where season length limits the time available to reach maturity (Higgins & Rankin 1996; Higgins 2000). To investigate this possibility, I measured the foraging investment and foraging success by *N. clavipes* from five univoltine populations inhabiting highly seasonal Mexican sites and from a bivoltine population inhabiting a less seasonal Panamanian site. This comparison revealed that relative foraging investment is sharply reduced in larger juveniles and adult females in populations from strongly seasonal habitats but not in the population inhabiting the relatively less seasonal habitat. I consider several possible proximate and ultimate causes for the reduction in foraging investment.

METHODS

Study organism.—*Nephila clavipes* is a large orb-web building spider distributed from the south-eastern United States to Missiones, Argentina. Juveniles of both sexes and mature females build large, fine-meshed orb-webs typically suspended in a less-orderly labyrinth of barrier silk (Levi 1980; Higgins 1992a). Orb webs are renewed nightly between 2300 h and 0500 h, the exact time varying among populations (Higgins & Buskirk 1992). Older juvenile and mature females do not always replace the entire orb. The proportion of the orb area that is replaced each night depends on immediate weather conditions and the devel-

opmental stage of the individual (Higgins & Buskirk 1992). The orb web is synthesized from proteins (the silk component) and water-soluble organic compounds that are precursors or derivatives of physiologically important compounds such as neurotransmitters and cell-membrane components (Vollrath et al. 1990; Townley et al. 1991; Higgins & Rankin 1999; Higgins et al. 2001). To investigate the effects of seasonality on investment into foraging, I compared data concerning prey capture success and orb web size (radius) from six populations of *N. clavipes*, one in a less-seasonal site in Panama and five in strongly seasonal sites in Mexico (Table 1). Voucher specimens are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D C.

Censuses and study sites.—I determined spider size and orb web investment during monthly or bimestrial censuses at each site. During the first census each year at each site, I located an area with at least 50 juveniles and returned to this area for subsequent censuses. At the end of each season when spiders were rare, I increased the total area searched. For each individual found, I made the following observations: spider size (leg I tibia-patella length, TPL, Higgins 1992b), proportion new silk in the orb ($\leq 1/3$, $\leq 1/2$, $\leq 2/3$, $\leq 3/4$, ≤ 1), maximum vertical orb radius (nearest 0.5 cm). In addition, I measured spiral strand density at Chamela, Nanciyaga, and Fortín de las Flores, counting the number of strands over two centimeters radius, ending 1 cm above the lower edge of the orb (Higgins & Buskirk 1992). I did not attempt to measure total capture area (as described in Herberstein & Tso 2000) for two reasons. First, the calculations are inappropriate for nephilid webs. The orb web of *Nephila* has branching radii, an exceedingly dense viscid spiral (Uetz et al. 1978) that varies in mesh size from hub to outer edge, and a shape that is strongly elliptical with little or no viscid spiral above the hub. Second, the measure of total capture strand is still an approximation that may not necessarily address the actual material investment into the orb. Spiders can and do vary the number of silk strands spun for a particular element of the web, resulting in webs that have the same physical dimensions but different material content as determined by dry weight of the web (pers. obs.). Observations

Table 1.—Climate data and seasonality of study sites. Climate data are from Garcia (1973), Bullock (1986) and Higgins (2000). Season length is determined as follows: seasonally cold sites–number of months with temperatures above 22 °C (coast), 20 °C (Fortín); seasonally dry sites–number of months with rainfall above 50 mm; Panama is distinct because, although dry and rainy seasons, the spiders are active throughout the year. The observed generation time is the number of months between peak number of unsexed juveniles and peak number of mature females in each year of the study, using midpoints if peaks were broad (from fig. 1, Higgins 2000). The population in Gigante Peninsula, Panama, is bivoltine with spiders present throughout the year.

Site	Coordinates	Altitude	Seasonality	Average season length (mo)	Observed generation time (mo)
Panama:					
Gigante Peninsula	9°N, 80°W	15 m	dry	12	dry: 6; wet: 6
Mexico:					
Playa Escondida	18°30'N, 95°W	5 m	cold	9	1989: 4.5
Nanciyaga	18°30'N, 95°W	100 m	cold	9	1989: 5; 1990: 4
Fortín de las Flores	19°N, 97°W	1000 m	cold	7	1989: 6; 1990: 5.5
Tehuacán	18°20N, 97°30'W	1500 m	cold, dry	5	1990: 3.5
Chamela	19°30'N, 105°W	50 m	dry	6	1989: 5; 1990: 3.5

on predation load are not included in the current paper because there were no significant differences in predation rates on juveniles among the populations used in the current study (pers. obs.). Predator attack rates on juvenile *N. clavipes* decline significantly when TPL > 0.7 cm (Higgins 1992a).

In 1983–1984, I conducted censuses on Gigante Peninsula, part of the research station operated by the Smithsonian Tropical Research Institute on Barro Colorado Island, Panama. This site is seasonally dry, but drought is mild and the population of *N. clavipes* is bivoltine with some spiders present throughout the year (Lubin 1978; Higgins 2000). In this study, each generation is labeled by the season in which it reaches maturity (i.e., the "rainy season" generation hatches in the dry season and matures in the early rainy season).

In 1989 and 1990, I conducted censuses in five sites along a transect spanning Mexico at approximately 19°N. The Mexican sites all have the same photoperiodicity, but differ in type of seasonality and in season length. Populations in all of the Mexican sites are typically univoltine, with the spiders emerging from the egg sacs as second instar juveniles at the initiation of the growing season (Hill & Christensen 1981; Higgins 2000). The various populations in Mexico experience qualitative-

ly different limits to the growing season. In seasonally cold sites (Playa Escondida, Nanciyaga, Fortín de las Flores), the growing season is limited by the arrival of strong cold fronts (nortes), which kill all individuals not protected within egg sacs. The first norte may arrive any time between early October and January and in some years, no nortes arrive at the coastal sites. The coastal populations at Playa Escondida and Nanciyaga are facultatively bivoltine (Higgins 1997). In Chamela, a seasonally dry site on the Pacific coast, the growing season is limited by the end of the rainy season, usually around October. The cessation of rains does not kill the spiders, and spiders may be found as late as three months after the last significant rainfall (Higgins 2000). Tehuacan, a mid-altitude desert in Puebla, has dry cold winters. Spiders in this site appear limited primarily by the arrival of the first norte (pers. obs.) and season length is estimated by temperature rather than rainfall.

Foraging success.—To determine the size range and diversity of insects captured, I recorded all cases of prey capture by spiders found during censuses and during prey capture surveys (see below). Prey observed to be in the orb web but ignored or actively rejected by the spiders were not included.

To determine diurnal prey-capture success at each site, I utilized dawn-to-dusk trap-line

surveys of spiders marked and measured the previous day (Turnbull 1962; Castillo & Eberhard 1983; Higgins 1987; Higgins & Buskirk 1992). I used a new group of spiders at new web sites in every survey. Each survey included at least 5 actively hunting animals within a circuit, such that I could visit all spiders within 15 minutes. The spiders observed during the survey were large juveniles (TPL ≥ 0.5 cm) and mature females. Spiders smaller than 0.5 cm TPL primarily capture very small insects requiring less than 15 minutes to consume, making the trap-line survey an inefficient method of recording foraging success. I estimated diurnal prey capture rates at least once each year at all sites except for Playa Escondida and Fortín de las Flores, where the surveys were run only in 1989. To test for variation in prey capture during the growing season, I made repeated surveys in Nanciyaga and Chamela in 1990 (3 and 2 surveys, respectively). These data are compared to published data on prey capture from Barro Colorado Island (Higgins & Buskirk 1992), as prey capture censuses were not conducted on Gigante Peninsula (separated from Barro Colorado Island by approximately 1 km).

Using Schoener's (1980) regressions of insect wet weight on body length for insects from tropical wet and tropical dry sites in Costa Rica, I estimated the total wet weight of prey captured by each spider during prey-capture surveys. Where prey were identified to order, I used the equation for that particular order. Hemiptera and Homoptera were not distinguished in my surveys and I used the equation from Hemiptera to estimate wet weight of these insects. I used the equations from the wet forest to estimate wet weight for insects captured in Playa Escondida, Nanciyaga and Fortin de las Flores and the equations from the dry forest to estimate wet weight of insects captured in Tehuacán and Chamela.

Statistical Analysis of Orb Size.—Orb radius as a function of spider size (TPL) is strongly heteroscedastic: variation in orb radius increases with increasing spider size (Higgins & Buskirk 1992). Square-root transformation of the orb radius effectively removed heteroscedasticity (Weisberg 1980), as was found in a prior analysis (Higgins & Buskirk 1992). Therefore, all subsequent analyses of orb web radius against spider size use square-root transformed data.

In all of the observations from the strongly-seasonal Mexican sites, orb radius was not a simple function of spider size but exhibited significantly reduced slope above TPL approximately equal to 0.5 (see below). Comparison of the investment into the orb among these populations involved three steps. First, I used ANCOVA to test whether the slopes above and below TPL = 0.5 cm were significantly different (all $P < 0.001$). Second, to test whether the function of orb size on spider size differed significantly between years, I assumed that the bend point was 0.5 TPL, split the data at this point, and used ANCOVA to test for differences between years for those populations observed in both years (Playa Escondida, Nanciyaga, Fortín and Chamela). Where there were significant differences between years, I determined the best-fit bend point separately for each year. When there was no difference between years, the data were pooled for comparisons among sites.

In order to quantitatively assess the location of the best-fit bend point, τ, I used Chappell's (1989) bend point analysis: using a series of values of the independent variable (spider size, TPL) as the bend point, separate regression analyses for data above and below each bend point were run and then the error sums of squares for the paired regressions were summed. The TPL value where the minimum summed ESS occurs is the best estimate of the bend point. In this analysis, intervals of 0.1 cm TPL were used.

Finally, to determine the similarity or dissimilarity among the populations, I used separate ANCOVAs to compare the regressions above and below the best-fit bend point of each population. Prior to running these final ANCOVAs, I verified that the preliminary tests for differences between years (which had used $\tau = 0.5$) were valid for the best-fit bend points.

RESULTS

Foraging success.—As has been observed earlier (Higgins & Buskirk 1992), larger spiders captured larger prey in all populations, but spiders of all sizes continued to capture prey in the smallest size category (≤ 2 mm). To compare prey size among populations, the observations were divided into three groups according to spider size: TPL < 0.5, 0.5 ≤ TPL < 1.0, 1.0 ≤ TPL. Prey were grouped

Table 2.—Diurnal prey–capture rates. Median prey size was determined from all observations of prey captured during censuses and surveys. Mean number of prey caught and mean weight of prey caught refer to prey capture per 12 h diurnal foraging and are calculated only from the prey capture surveys. Panama prey capture data from Higgins & Buskirk (1992). Fortín mean weight of prey captured estimated from juvenile spider numbers of prey captured (Table 2a) and large spiders' median prey size; see text for details. [1]a posteriori F tests; within groups $P > 0.3$, among groups $P < 0.03$; Panama and Fortín data were not included in statistical analyses.

Site, year	Surveys (n)	Spiders (n)	Median prey size, mm (n)	Mean number (SE)	Mean weight, mg (SE)
a. Juvenile spiders (0.5 < TPL ≤ 1.0 cm)					
Nanciyaga 1990	1	14	4 (55)	2.5 (0.43)	1.41 (0.38)
Fortín 1989	1	14	2 (29)	3.8 (2.6)	1.16 (0.23)
Chamela 1990	1	14	4 (23)	1.6 (0.44)	0.99 (0.37)
b. Large juvenile and adult female spiders (TPL ≥ 1.0 cm)					
Playa Escondida 1989	1	14	4 (13)	1.2 (0.30)	4.48 (3.30) a
Nanciyaga 1989	1	12	6 (59)	3.1 (0.62)	5.11 (2.32) a
1990	2	37	5 (124)	3.4 (0.31)	9.14 (2.09) a
Fortín (estimated)	0	0	6 (24)	4 (—)	6.84 (—)
Tehuacán 1990	1	9	10 (23)	3.0 (0.75)	17.44 (5.12) b
Chamela 1989	1	12	4 (58)	2.5 (0.60)	1.41 (0.41) a
1990	1	10	5 (26)	1.9 (0.28)	4.82 (2.94) a
BCI, Panama 1983 rainy	2	26	8	1.8 (9.8)	6.4 (6.7)
BCI, Panama 1983 dry	2	10	6	1.4 (1.1)	1.9 (3.2)

into 2 mm size classes (pooling larger size classes to reduce the number of empty cells). For the largest spiders, there were no differences between years in Chamela or Nanciyaga (maximum likelihood $\chi^2 < 5.5$, $P > 0.37$). Pooling across years for each site, comparisons revealed among-site differences in the size of prey captured by the largest spiders, but no differences in the size of prey captured by the smallest and intermediate-sized spiders (maximum likelihood χ^2 test: TPL < 0.5, $\chi^2 = 9.19$, $df = 8$, $P = 0.33$; $0.5 \leq$ TPL < 1.0 $\chi^2 = 10.97$, $df = 9$, $P = 0.28$; TPL ≥ 1.0 delta $= 0.5$, $\chi^2 = 39.97$, $df = 16$, $P = 0.001$).

Within sites, there was very little variation between years or among repeated surveys in number of prey captured per spider per day (Table 2). In Chamela and Nanciyaga, diurnal prey capture did not vary significantly among surveys in 1990 (ANOVA of log-transformed number of insects captured/spider/survey; Chamela: $F_{(1,22)} = 1.23$, $P = 0.28$; Nanciyaga: $F_{(2,48)} = 0.92$, $P = 0.41$), or between 1989 and 1990 (Chamela: $F_{(1,34)} = 0.89$, $P = 0.35$; Nanciyaga: $F_{(1,61)} = 0.07$, $P = 0.80$). Therefore, observations within each site were combined for comparisons among sites. Diurnal prey capture rates varied among sites ($F_{(4,131)} = 4.83$, $P = 0.001$), being significantly lower at

Playa Escondida (a posteriori contrast: $F_{(1,131)} = 10.37$, $P = 0.002$), and somewhat lower at Chamela than the other three sites.

The wet-weight of prey captured per spider per day varied among sites for the larger females, but did not vary among sites for the smaller spiders (Table 2). Because larger spiders capture larger prey, I compared total wet weight of prey captured among sites separately for surveys with intermediate sized spiders (0.5 cm $\leq$ mean TPL < 1.0 cm) and surveys with large spiders (mean TPL ≥ 1.0 cm). Three prey-capture surveys were conducted for intermediate-sized spiders: Fortín de las Flores (August), Nanciyaga (May), and Chamela (August). These spiders captured on average 1 mg prey/diurnal survey at all three sites (ANOVA: $F_{(2,39)} = 0.39$, $P = 0.68$). The large spiders captured significantly different amounts of prey at the different sites (Table 2; comparing Playa Escondida, Nanciyaga, Tehuacán, Chamela. ANOVA: $F_{(3,89)} = 3.79$, $P = 0.013$). This appears due largely to the very high prey capture rate and large median prey size at Tehuacán (a posteriori contrast of wet weight captured: Chamela vs. Tehuacan, $F_{(1,89)} = 10.22$, $P = 0.001$; [Playa Escondida and Nanciyaga] vs. Tehuacan $F_{(1,89)} = 5.86$, $P = 0.002$). Due to problems obtaining the con-

tinuous access required for prey-capture surveys, no prey capture surveys were conducted at Fortín de las Flores during the period when larger females were present in the population. For subsequent comparisons among populations, I estimated wet weight of prey captured by large females in Fortin in the following manner: median prey size caught by spiders TPL $\geq$ 1.0 was 6 mm in Fortin ($n = 13$), and the mean weight of 6 mm prey in Fortin was 1.71 (SE = 0.11). Assuming that the mean number of prey captured per diurnal survey by juveniles, 4 insects, is constant over the season (as observed in Chamela and Nanciyaga), the wet weight of prey captured per day in Fortín by the larger females can be estimated as 6.84 mg.

Foraging Investment.—Foraging investment is altered by three aspects of orb-web structure: proportion of new silk in the orb, spiral strand density, and orb web size. The variation in proportion of new silk spun each day is not considered in the current paper, as it did not differ from what has been described elsewhere (Higgins & Buskirk 1992). Larger spiders are more likely to partially renew the orb web, and the radius of partially renewed orbs is larger than the radius of wholly renewed orbs by spiders of the same size. Therefore, I included only completely renewed orbs (more than 75% new) in the comparison of orb size and spiral strand density among the sites.

Examination of the relationship between orb radius and spider size (taking the square root of orb radius to reduce heteroscedasticity) revealed a different pattern in Panama compared to all Mexican sites (Figs. 1, 2). In Gigante, Panama, orb size increased with increasing spider size, and the relationship between orb size and spider size did not differ between the two generations (Table 3a). Pooling across generations and comparing orb-web investment between large and small spiders showed no difference in slope (Table 3b): orb radius (square-root transformed) was a simple straight-line function of spider size (Fig. 1). In contrast, in all Mexican populations, larger spiders built smaller orbs that would be expected from extrapolating from the observed investment by small juveniles (Fig. 2).

Prior to determining the best-fit bend point, τ, for the Mexican populations, I tested for differences between years at each site assum-
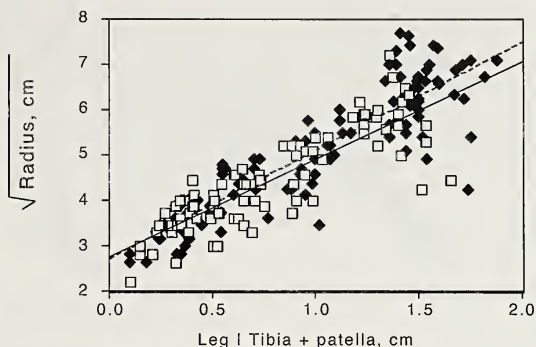

Figure 1.—Orb radius (square root transformed) as a function of *Nephila* size (TPL) in Gigante Peninsula. Black diamonds (dash line): wet season; the generation maturing in the early rainy season; white squares (solid line): dry season; the generation maturing in the early dry season. There is no difference in orb size between the generations.

ing a bend point of TPL = 0.5. These preliminary analyses revealed significant differences in slope between years for smaller spiders at Fortín de las Flores and for larger spiders at Playa Escondida (ANCOVA. Fortín: small spiders $F_{(1,256)} = 5.32$, $P = 0.022$ and large spiders $F_{(1,74)} = 0.119$, $P = 0.73$; Playa Escondida: small spiders $F_{(1,162)} = 0.239$, $P = 0.625$ and large spiders $F_{(1,49)} = 5.92$, $P = 0.02$). Although there was a significant difference between years among large spiders at Chamela, this was most likely due to absence of observations between TPL = 0.4 and TPL = 0.7 for 1989 (Fig. 2), and I dropped the Chamela 1989 observations from the subsequent analyses of orb size. Preliminary analyses revealed no differences between years at Nanciyaga (small spiders $F_{(1,72)} = 1.699$, $P = 0.20$ and large spiders $F_{(1,124)} = 0.116$, $P = 0.73$). In all cases, where there was no difference between slopes there was also no difference in intercept (all year effects $P \geq 0.06$).

Because there were significant differences in the slopes between years observed at Fortín de las Flores and Playa Escondida, I considered the 1989 and 1990 data separately when determining the best-fit bend point, τ, for these data sets (Table 4). I first compared the best-fit bend points to the *a priori* estimate of τ = 0.5 cm using *t*-tests. At all sites except Fortín in 1990, the value of τ was not statistically different from TPL = 0.5 cm (*t*-test: all $P \geq 0.5$; Table 4). In Fortín in 1990, the bend point occurred at a significantly smaller spider
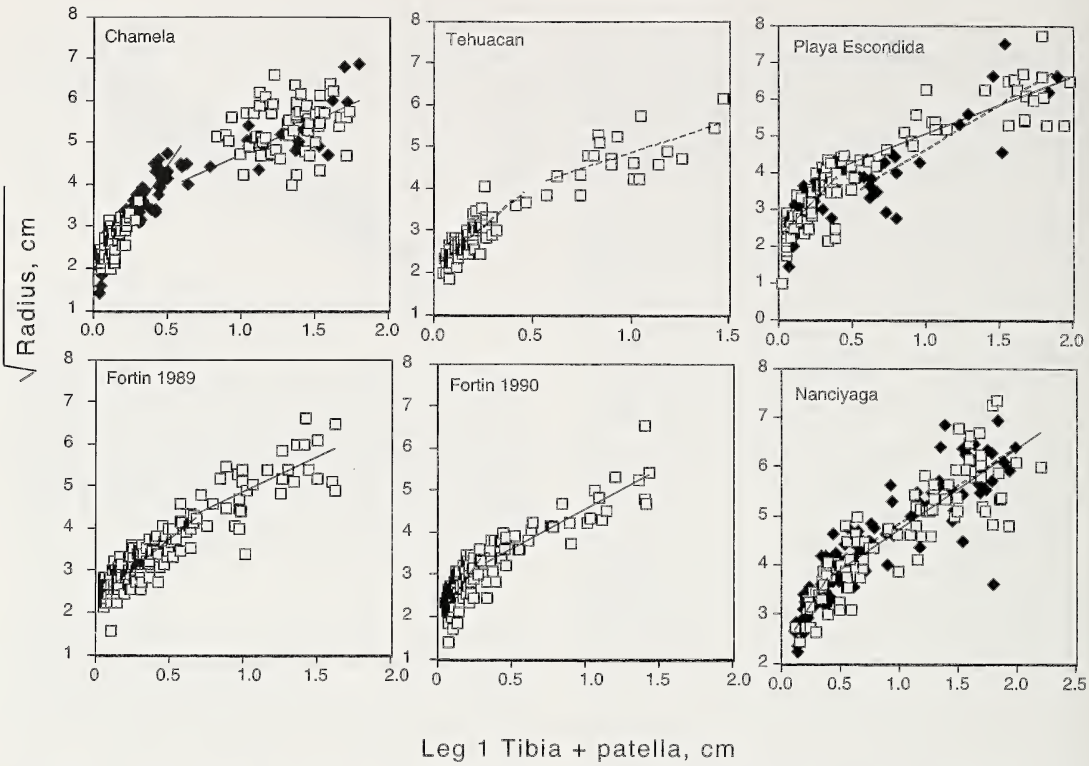
Leg 1 Tibia + patella, cm

Figure 2.—Orb radius (square root transformed) as a function of *Nephila* size (TPL) in Mexican populations. Where two years of data are plotted in the same graph (Chamela, Nanciyaga, Playa Escondida), squares (solid line):1989; diamonds (dashed line):1990. No regression is plotted for the Chamela 1989 data as there is a gap in the data between TPL of 0.4 and 0.7, but the data are presented for comparison.

Table 3.—Orb web size as a function of spider size in Gigante, Panama, where y is the square root of orb radius and x is leg I tibia + patella length.

a. Comparison of generations

Dry season	y = 2.78 + 2.11 x			$F_{(1,105)} = 190.35$	$P < 0.001$
Rainy season	y = 2.88 + 2.21 x			$F_{(1,54)} = 102.58$	$P < 0.001$

ANCOVA

Source	SS	df	F	P
TPL	96.29	1	294.73	< 0.001
Generation	0.044	1	0.14	0.71
TPL x gen	0.05	1	0.15	0.70
Error	51.95	159		

b. Comparison of spiders smaller and larger than TPL = 0.5 cm

TPL < 0.5 cm	y = 2.49 + 2.98 x			$F_{(1,54)} = 35.68$	$P < 0.001$
TPL ≥ 0.5 cm	y = 2.76 + 2.25 x			$F_{(1,205)} = 184.37$	$P < 0.001$

ANCOVA

Source	SS	df	F	P
TPL	14.37	1	43.56	< 0.001
Size class	0.251	1	0.76	0.39
TPL x class	0.282	1	0.85	0.36
Error	52.45	159		

Table 4.—Values of best-fit bend points, τ, and 95% confidence intervals (CI) for each population. * In Fortín in 1990, τ is significantly different from 0.5 ($t = 2.509$, $P < 0.05$).

Site	τ	95% CI
Playa Escondida 1989	0.4	0.079
Playa Escondida 1990	0.5	0.184
Nanciyaga	0.4	0.078
Fortín 1989	0.7	0.125
Fortín 1990	0.3*	0.046
Tehuacán 1990	0.5	0.106
Chamela 1990	0.6	0.069

Table 5.—Analysis of foraging investment: Analysis of covariance of orb-web size among populations, with spider size as covariate. a include data from Playa Escondida, Nanciyaga, Fortín 1989, Fortín 1990, Tehuacán, Chamela; b include data from Playa Escondida 1989, Playa Escondida 1990, Nanciyaga, Fortín, Tehuacán, Chamela.

Source	df	Mean square	F	P
a. Spiders with TPL < τ				
TPL	1	75.201	760.26	<0.001
Site	5	0.874	8.84	<0.001
TPL × site	5	1.881	19.02	<0.001
Error	607	0.099		
b. Spiders with TPL ≥ τ				
TPL	1	75.01	256.17	<0.001
Site	5	1.45	4.95	<0.001
TPL × site	5	0.86	2.93	0.013
Error	327	0.29		

size. Prior to running ANCOVA comparisons among populations, I also tested whether the differences between years found at Fortín de las Flores and Playa Escondida using *a priori* assumption of $\tau = 0.5$ persisted with the best-fit bend point, by repeating the ANCOVA analysis comparing the slopes of the regression of orb-web radius on TPL between years for each site. In both cases, the results were the same: there were significant differences in slope between years for large spiders at Playa Escondida and small spiders at Fortín. For all subsequent tests, I kept the data of these sites separated by year.

In all of the Mexican sites, the rate of increase of orb radius with spider size decelerated significantly in spiders larger than TPL = 0.5. Further comparisons among Mexican populations therefore considered spiders of TPL < τ separately from spiders of TPL ≥ τ. The analyses of covariance for orb radius by spiders of TPL < τ and spiders of TPL ≥ τ revealed significant interactions between spider size and site, indicating that the slopes of the regressions were significantly different among sites (Tables 5, 6). However, a posteriori comparisons show that the significance of the population x TPL factor is due to grouping of the populations rather than unique foraging investments in each population. Among spiders TPL < τ, those in Fortin de las Flores in 1989 increased orb-web size more slowly (lower slope) than any other population (Table 6a). Among spiders TPL ≥ τ, the populations split into two groups (Table 6b). Even where significant, the differences among these populations are much less than the differences between large and small spiders. Comparing Fortin de las Flores (1989) to Chamela (1990;

the highest slope), the slope in Fortin is 43% of the slope found for Chamela. Similarly, comparison of the lowest and highest slopes for spiders TPL ≥ τ (Tehuacan vs. Playa Escondida) revealed 37% difference. All within-population decelerations were greater (Table 6b).

There remains the possibility that the spiders in a given population always invest more in the orb, even if the relative investment declines with increasing spider size. This would be reflected as concordance between the small and large spiders (< ≥ τ) in each population across all populations. To test for concordance, I used Kendall's coefficient of concordance (Siegel & Castellan 1988), comparing the rank orders of populations according to the slopes from the regression analyses of orb size on spider size.

The slopes of the regressions on either side of the bend point vary with the actual point at which each data set is split into two groups, therefore I first ran a sensitivity analysis testing for changes in rank-order of populations when altering the value of τ. I divided each data set at the maximum and minimum of the 95% confidence interval around each best-fit bend point and calculated the slopes for small and large spiders (keeping the years separate for Playa Escondida and Fortín). I then compared the rank orders of the populations for large or small spiders among three sets of

Table 6.—Analysis of foraging investment: regression equations of orb-web size on spider size for all Mexican sites. Letters (a, b) in the regression column refer to groups with *slopes* that are not significantly different. Small spiders: within group a, interaction effect $F_{(4,455)} = 0.86$ adjusted $P = 0.97$; between groups interaction effect $F_{(1,622)} = 62.43$ adjusted $P < 0.002$. Large spiders: within groups, interaction effect (a) $F_{(2,204)} = 0.022$, adjusted $P = 0.99$; (b) $F_{(2,116)} = 1.58$, adjusted $P = 0.21$. Between groups interaction effect $F_{(1,328)} = 9.92$, adjusted $P = 0.004$. The percent change is calculated as the change from high slope to low slope as a percent of the larger slope.

a. Spiders with TPL $< \tau$

Site	Regression	R^2	Rank order of slopes
Playa Escondida 1989	y = 2.21 + 4.22 x **a**	0.59	5
Playa Escondida 1990	y = 2.17 + 4.47 x **a**	0.66	6
Nanciyaga	y = 2.22 + 3.95 x **a**	0.55	4
Fortín de las Flores 1989	y = 2.31 + 2.96 x **b**	0.77	1
Fortín de las Flores 1990	y = 1.93 + 3.69 x **a**	0.54	2
Tehuacán	y = 2.11 + 3.93 x **a**	0.63	3
Chamela 1990	y = 1.88 + 5.22 x **a**	0.89	7

b. Spiders with TPL $\geq \tau$

Site	Regression	R^2	Rank order of slopes	% change
Playa Escondida 1989	y = 3.48 + 1.57 x **a**	0.74	2	−62%
Playa Escondida 1990	y = 2.19 + 2.43 x **b**	0.70	7	−46%
Nanciyaga	y = 3.20 + 1.59 x **a**	0.68	3	−60%
Fortín de las Flores 1989	y = 3.21 + 1.65 x **b**	0.38	4	−44%
Fortín de las Flores 1990	y = 2.66 + 1.89 x **b**	0.76	5	−49%
Tehuacán	y = 3.31 + 1.53 x **a**	0.39	1	−61%
Chamela	y = 2.64 + 1.92 x **b**	0.31	6	−63%

slopes (breaking the data at the best τ, lowest τ and highest τ). Kendall's coefficient of concordance showed significant concordance among the rank orders for both the small and the large spiders (small spiders: Kendall's coefficient = 0.73, $df = 6$, $P = 0.041$; large spiders: Kendall's coefficient = 0.92, $df = 6$, $P = 0.011$). This indicates that the rank order of populations according to relative orb size (slope) is insensitive to the exact position of the bend point in each data set. I then tested for rank-order concordance between small spiders and large spiders in each population using the slopes calculated with the best-fit τ. Among the Mexican sites, there is no correlation among populations between large and small spiders (Table 6; Kendall's coefficient = 0.696, $df = 6$, $P = 0.21$).

It is possible that the change in rate of increasing orb size with growth is correlated with a shift in orb-mesh size, resulting in a constant material investment. If this is the case, then I expect a similar "bent line" pattern in orb-mesh density with increasing spider size. To test this, I compared mesh density for spiders of different sizes in three sites with strong "bends" in orb-web radius: Chamela, Fortín de las Flores and Nanciyaga. There was significant variation among sites (Fig. 3). In all populations, spiral strand density declines with increasing spider size. Among these sites, the decline was steepest at Fortín and shallowest at Chamela (Fig. 3). There is no indication that the relationship is not a simple straight line.

DISCUSSION

When environmental factors other than foraging success, such as short season length, limit the probability of successful survival or reproduction, these factors may alter the decisions of resource allocation into foraging, especially when variation in foraging success is included in the analysis (Caraco 1980; Houston & McNamara 1982; Stephens & Charnov 1982; Johansson & Rowe 1999). Such factors have been taken into account in some models, such as risk-sensitivity models (reviewed in Stephens & Krebs 1986) and state-sensitive models (Mangel & Clark
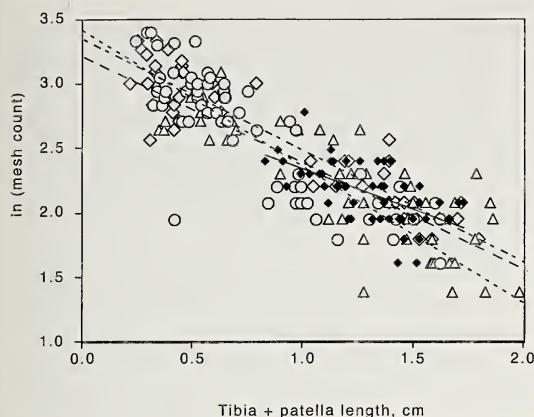
Figure 3.—Spiral strand density vs. *Nephila* size (Leg 1, TPL), new orbs only, for three Mexican populations. Triangles (dashed line): Nanciyaga 1989; circles (dotted line): Fortín 1989; black diamonds (solid line): Chamela 1989; and open diamonds (dot-dash line): Chamela 1990. Although there are significant differences among sites in slope and intercept (slope: $F_{(2,164)} = 4.16$, $P = 0.017$; intercept: $F_{(2,164)} = 3.70$, $P = 0.027$), the relationship of strand density to spider size is a simple straight line.

1988). One important result from these models is that short-term optimization strategies may not maximize fitness. Rather, animals are predicted to alter their foraging strategy based upon the probability of gaining sufficient energy to survive and reproduce. Most of these models, however, still only consider the foraging behavior of a single developmental stage. Resource allocation decisions occur throughout development. Consideration of the fitness consequences of developmental changes in resource allocation will improve our understanding of the long-term affects of variation in resource use (Perrin & Sibley 1993). Investigation of orb size over the entire developmental period of juvenile *N. clavipes* revealed that the relative investment into foraging is not necessarily constant: in populations inhabiting strongly seasonal areas, relative orb-web investment declined as spiders grow. This deceleration in foraging investment was not correlated with shifts in orb renewal or with changes in mesh size. Comparison with the bivoltine population in Gigante (current paper) and the 1985 observations from the facultatively bivoltine population in Los Tuxtlas (Higgins & Buskirk 1992) indicate that the shift in allocation to

foraging effort may reflect changes in priorities that are influenced both by seasonality and by foraging success.

Proximally, changes in orb-web structure might cause changes in orb-web size. Orb radius in *N. clavipes* is negatively correlated with the amount of new silk and spiral strand density, and larger spiders tend to build widely-meshed, incompletely renewed orbs (Higgins & Buskirk 1992). However, these factors cannot explain the observed sudden deceleration in foraging investment. Although the bend point occurs at about the size at which the spiders become more likely to partially renew the orb (Higgins & Buskirk 1992), only data from completely renewed orbs were included in the present analyses. Nor is this a reflection of a shift in mesh size, as strand density is a simple linear function of spider size.

Among the Mexican sites visited in 1989–1990, the striking pattern is how little variation there is among populations. Among smaller spiders, spiders of a given size built significantly smaller webs at Fortín in 1989 compared to other sites, but no environmental factors are correlated with this: prey capture is higher in number, but lower in median weight resulting in no significant difference in mean weight of prey captured. Comparing the larger spiders among populations and between years in Mexico, the populations fell into two distinct groups but again there are no correlated differences either in prey capture (only Tehuacan differed in prey capture) or season length. By comparing data across a larger time and geographic scale, the possible roles of both factors in determining resource allocation can be tentatively described.

Marginal increases in resource allocation to weight gain and development will be favored if they result in marginal increases in fitness (Perrin 1992). There are two arguments for why shifting resources from foraging to growth could increase female fitness. First, decreases in orb investment may not decrease prey capture (Higgins & Buskirk 1992), so holding web size relatively constant after a certain size is achieved may not greatly alter the probability of foraging success. Second, there are great fitness advantages of early maturation and of large female size. It is notable that the developmental stage at which the spiders in Mexico decreased relative investment

into the orb web, approximately the fifth juvenile instar, is long before female maturation. At this developmental stage, most males have reached sexual maturity but females will pass through three or more additional instars prior to maturing. Under high rates of weight gain, fifth instar females need at least 36 days to mature, and then 21 days to lay the first egg sac (Higgins 2000, 2002). Spiders in strongly seasonal environments must reproduce prior to the end of the season.

Comparison among these univoltine Mexican populations, the bivoltine population in Panama, and the 1985 observations from Los Tuxtlas (a mild year in coastal Veracruz with very high prey capture; Higgins & Buskirk 1992) better illustrate the potential importance of both season length and prey capture success in determining allocation of resources to web building. The comparison of orb-web size between the population in Gigante, Panama, and populations in Mexico supports the hypothesis that the animals in strongly seasonal environments may be shifting resources away from foraging to improve the chances of reproduction. The prey-capture success recorded in Panama falls within the range of observations from the Mexican sites (Table 2), but the climate is much less seasonal. Although this region of Panama is seasonally dry, one generation of spiders hatches, emerges, and passes through several instars during the dry season and the end of the rains does not kill larger juveniles and mature females of the next generation. Thus, the seasonality does not strongly affect the life cycle, nor was there any reduction in female fecundity associated with delayed maturation (Higgins 2000). With no penalty for delayed maturation, there was also no pattern of reduced investment to orb-web building as spiders in this site grew.

Prey capture success is also apparently important in determining developmental patterns of resource allocation to orb building. Los Tuxtlas field station (UNAM) is within 20 km of Nanciyaga and Playa Escondida and has similar climate and forest structure (it was not used in the current study due to local, temporary reduction in spider abundance; pers. obs.). During a 1985 study, the spiders in Los Tuxtlas captured nearly twice as much prey compared to prey capture for spiders in the same region in the current study (ca 12 mg/day in 1985 vs. ca 5 mg/day in 1989 and 9

mg/day in 1990) and there is no indication in the 1985 data of any change in the relative investment into the orb during the course of development (Higgins & Buskirk 1992). It is potentially important that the end of the season at these sites, governed by the arrival of the northern storms (nortes) is apparently unpredictable.

One can gain a sense of the relative importance of prey capture rates and seasonality by comparing the 1985 data from coastal Veracruz with the 1990 data from Tehuacán. Although the growing seasons at both Tehuacán and coastal Veracruz end with cold temperatures, the nortes do not always reach central Veracruz and these populations are facultatively bivoltine (Higgins 1997). In contrast, the Tehuacan growing season is predictably short and always terminated by cold winter temperatures (Higgins 2000). In 1990, spiders in Tehuacan had even higher prey capture success than Los Tuxtlas in 1985, but the Tehuacan spiders still exhibited a very strong decline in orb-web size.

These results are very different from similar, experimental, results of foraging investment under time constraints in the damselfly larvae (Johansson & Rowe 1999). In these actively hunting predators, time constraints resulted in increased investment into foraging. The difference may reflect the more direct competition for resources between web and body in the spider, or differences in variation in success with similar foraging investment. First, there are direct trade-offs in materials between orb-web synthesis and growth and development in *N. clavipes* juveniles (Higgins & Rankin 1999). Web components such as protein and choline are required for web construction as well as for physiological functions. Second, building a larger orb web does not necessarily increase chance of foraging success. Increased foraging effort (time and energy spent searching) by active foragers may have a less direct impact upon growth and a more certain pay-off. Only further research in a wider array of foragers will determine if this dichotomy is widely applicable.

Life-time strategies of allocation of resources among different, conflicting requirements during growth, development and reproduction are indicated by these observations to be more complex than what can be modeled as extensions of short-term optimization strategies.

Optimization theory (reviewed in Perrin & Sibly 1993) can provide a conceptual framework for experimental examination of resource allocation, as applied to plants by Iwasa & Roughgarden (1983). Such models are more difficult to apply to animals, as the measurement of allocation into different organ systems is usually destructive. Web-building spiders, with a physical record of the decisions regarding foraging investment, may prove more amenable to the study of the interface between life-history strategies and behavioral strategies.

ACKNOWLEDGEMENTS

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NATURAL HISTORY OF *GLENOGNATHA EMERTONI* (ARANEAE, TETRAGNATHIDAE): MATING BEHAVIOR AND SPERM RELEASE IN A HAPLOGYNE

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ABSTRACT. *Glenognatha emertoni* (Simon 1887) is a small haplogyne orb-weaver collected near streams and dry streambeds in southern Arizona whose habits are unknown. Field observations revealed that *G. emertoni* are commonly found in vegetation overhanging streams and, more rarely, under streamside rocks. Mating pairs were observed on or near adult female webs. Males lack mate-guarding behavior and leave the female immediately after copulation. To examine mating behavior in a controlled setting, juveniles and adults were collected from the field and maintained in the lab. Matings were arranged between wild-caught adults and also between laboratory-reared virgins in order to describe mating behavior and sperm release during copulation. Unlike most other orb-weaving spiders studied, the number of sperm released and overall duration of copulation are not influenced by female mating history in *G. emertoni*. Male *G. emertoni* release equivalent numbers of sperm to virgin and non-virgin females. Given this pattern of sperm release and the lack of mate-guarding behavior by males, sperm competition should be intense in this species. Based only on the numbers of sperm released by each male in the study, doubly-mated females would be expected to produce egg sacs of mixed paternity, if all else were equal.

Keywords: Araneae, sexual selection, sperm competition, spermatheca, spider

Glenognatha emertoni (Simon 1887) is a small, haplogyne tetragnathine orb-weaver (adult body length 4.5–5 mm) known from Arizona and New Mexico (Map 8, Levi 1980). The habits of *G. emertoni* are unknown. The genus *Glenognatha* includes 20 named species from the Americas (North, Central, and South), Africa, and the Caribbean, Galapagos, and Pacific Islands, but it is possible that many tropical species remain undescribed (Hormiga & Döbel 1990; Platnick 2006). This genus is a member of the sub-family Tetragnathinae, a haplogyne clade within the entelegyne family Tetragnathidae (Hormiga et al. 1995). Within the tetragnathines, the mating behavior of species in the haplogyne genera *Tetragnatha* and *Pachygnatha* have been well-described (Gerhardt 1921, 1927; LeSar & Unzicker 1978; Huber 1998; West & Toft 1999; Danielson-François 2002; Danielson-François & Bukowski 2005). However, the behavior of species within the haplogyne genus *Glenognatha* is essentially unstudied apart

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from Barrows (1919) observations of *Glenognatha foxi* (McCook 1894) and a single published note by Edwards & Senske (2001) on the mating behavior of *Glenognatha heleios* (Hormiga 1990), a recently discovered species (Hormiga & Döbel 1990).

Haplogyne taxa are especially intriguing to study because they provide a counter-point to studies on entelegynes, arguably the largest and most well-researched group of spiders. Haplogyny is the basal condition in the Araneomorphae and haplogynes are defined, in part, by their simple genitalia (Wiehle 1967). In particular, haplogyne females have *cul-de-sac* spermathecae with one duct for insemination and fertilization (Simon 1895). Entelegyne females have more complex conduit spermathecae, each with a specialized duct for insemination whose opening is located externally in the epigynum, and a separate duct for fertilization (Simon 1895). Although they are located within the entelegyne suborder (Hormiga et al. 1995; Griswold et al. 1998, 1999), a reversal to haplogyny has occurred within the tetragnathines (Wiehle 1967), which have *cul-de-sac* spermathecae with one duct for insemination and fertilization (Danielson-François 2002).

Such morphological differences in female spermathecae might underlie the diversity of paternity patterns in spiders, which range from first- to last-male advantage—unlike the last-male advantage common to insects, whose spermathecae often resemble a simple *cul-de-sac* (Walker 1980; reviewed in Simmons & Siva-Jothy 1998; Elgar 1998; Eberhard 2004). To explain this diversity, Austad (1984) proposed that spermathecal morphology and ejaculate stratification generated first-male advantage in entelegynes and last-male advantage in haplogynes. Austad (1984) also argued that haplogyne males would be indifferent towards, but that entelegyne males would prefer, virgin females as mates and that haplogyne males would guard mates after copulation. To date, mate-guarding, mating behavior, and paternity have been studied in relatively few haplogyne taxa.

Post-copulatory mate-guarding should be common in haplogyne taxa if Austad's (1984) predictions hold. Of the haplogyne species studied thus far, co-habitation of adult pairs has been found in seven pholcid taxa (Eberhard & Briceño 1983; Eberhard et al. 1993; Blanchong et al. 1995; Kaster & Jakob 1997). Contrary to Austad's hypothesis, in at least one pholcid species males co-habit equally with penultimate-molt and mature females (Eberhard et al. 1993). Yet overall, a strong preference for co-habitation with penultimate-stage females, rather than mature females, appears to be lacking in the pholcid species studied (Eberhard et al. 1993). Of the *Tetragnatha* species examined, both co-habitation and mate-guarding appear to be absent; males leave the female immediately after copulation (West & Toft 1999; Danielson-François 2002; Danielson-François & Bukowski 2005; but see LeSar & Unzicker 1978). No information on the co-habitation or mate-guarding behavior of *Glenognatha* species is available at present.

Austad (1984) predicted that last-male paternity advantage would be common among haplogyne taxa, but empirical evidence to date offers equivocal support. Paternity patterns have been examined in three pholcids and one *Tetragnatha* species (reviewed in Elgar 1998; Eberhard 2004). A last-male biased paternity pattern has been shown for *Pholcus phalangioides* (Fuesslin 1775), *Holocnemus pluchei* (Scopoli 1763), and *Tetragnatha extensa* (Linnaeus 1758) (Yoward 1996, 1998; Kaster & Jakob 1997; West & Toft 1999; Schäfer & Uhl 2002). In contrast, *Physocyclus globosus* (Taczanowski 1873) has a paternity pattern that does not significantly differ from random sperm mixing (Eberhard et al. 1993). Haplogyne paternity patterns generally exhibited a high level of variation within a species: males sired from 0 to 100% of the progeny—similar to other spider paternity studies (reviewed in Elgar 1998). Even within an individual female, paternity patterns may vary: subsequent egg sacs from mated *T. extensa* females generally revealed an anti-chronological order of mating priority; however, a series of egg sacs from individual females defied any such general rules (West & Toft 1999). From these studies, it seems clear that paternity patterns are highly variable both within and among haplogyne species.

Although many different factors certainly underlie these complex behavioral and paternity patterns (e.g., cryptic female choice; Eberhard 1996, 2004), differences in sperm release among males might explain part of the variation. The amount of sperm transferred by males to virgin and non-virgin females may vary, as has been demonstrated in several entelegyne taxa in which males release little or no sperm to non-virgin females (Christenson & Cohn 1988; Andrade 1996; Bukowski & Christenson 1997; Bukowski et al. 2001). In contrast, the only data available for a haplogyne species thus far showed that males release equivalent numbers of sperm to virgin and non-virgin females (Danielson-François & Bukowski 2005). Data from only one species prevents generalizations about haplogyne sperm release behavior: more research on haplogyne species is needed.

This study focused on an Arizona population of *G. emertoni* from the Huachuca mountains, an appropriate location because the type specimen for the species was also collected in southeastern Arizona (Levi 1980). Here, I describe the natural history and mating behavior of *G. emertoni*, while offering the second demonstration of sperm release behavior in a haplogyne species.

METHODS

Natural History and Collection.—Previous records for *Glenognatha emertoni* stated that specimens were collected under rocks

near streams or in dry streambeds in the southern corner of Arizona and New Mexico (Levi 1980). Over the course of this study, approximately 175 immature, penultimate-molt and adult *G. emertoni* were collected from vegetation overhanging streams in mid-elevation riparian areas in the Huachuca Mountains of southeastern Arizona (31°28′N, 110°20′W). Voucher specimens were deposited in the arthropod collection of the Department of Entomology, University of Arizona, Tucson, Arizona 85721 USA. Of the spiders collected, 40 penultimates were brought into the laboratory, and reared to adult stage in individual 20 ml polystyrene vials from March–May 2000. Spiders were fed *ad lib.* daily on fruit flies (*Drosophila melanogaster*) and walnut flies (*Rhagoletis juglandus*). The animals were observed daily, and the date of molting was recorded. Adult virgins were used in staged mating experiments in the laboratory. Several wild adults were collected from March–May 2000 and additional wild adults were collected from March–April 2001. Collection sites were far downstream of field observation areas in order to avoid influencing the natural behavior of individuals at the observation sites.

Field observations of mating behavior were recorded during the late afternoon into the early evening (15:00–22:00 h) on 31 April and 2, 4, 6 May 2000 under ambient light conditions whenever possible. Occasionally, when natural light was insufficient for observations, a flashlight also was used. When used, the flashlight was not focused directly on the spiders, but directed instead at the substrate beneath the web such that the individual was silhouetted against a brighter background. Two females on webs with males nearby were observed each evening. Web surfaces were horizontal (or nearly so) and built directly above the stream, usually within five cm of the water surface. Field observations of mating behavior were comparable to the results obtained in the laboratory, suggesting that the staged matings were an appropriate surrogate.

Procedures for Staged Matings.—Laboratory-reared virgin males were at least three days post-molt before being used in staged matings to ensure they had inducted sperm into their palps. Prior to mating, virgin laboratory-reared females that were at least seven days post-molt were individually placed into

glass aquaria (30.5 × 15.0 × 20.5 cm) containing about 4 cm of water and several twigs. Females were allowed five minutes to settle onto their twig before a randomly chosen male was placed nearby. All encounters were videotaped with a NEC color CCD camera model NX18A with attached macro lens (Micro Nikkor Nikon 105 mm) mounted on a wooden platform with a Bogen ball head for camera rotation. During recording, live signal was relayed to a monitor, resulting in ~20× magnification. Similar to other tetragnathine species studied, *G. emertoni* also use chelicerae as holdfasts to steady the pair as the male inserts his pedipalps during mating. After copulation, staged encounters were considered terminated when the pair disengaged chelicerae and retreated from one another for at least 15 min. Pairs have never been observed to resume copulation more than 15 min after cheliceral disengagement (Danielson-François pers. obs.). If mating did not occur within 15 min, the previous male was removed and a new male was introduced to the mating arena until mating occurred. Adult females were mated to two adult males within fifteen minutes of each other. Males were immediately frozen and stored at −80° C for sperm quantification. Procedures for mating wild-caught males to wild-caught females were similar to those described above for mating laboratory-reared virgins.

Videotapes were later transcribed and latency to cheliceral engagement (in sec), latency to courtship after cheliceral engagement (in sec), which palp was inserted (left or right), duration of palp insertion (in sec), number of insertions, and total time spent *in copula* (in sec) were recorded. Palp insertion was defined as the complete insertion of the tip of the embolus into the female's gonopore that was succeeded by at least one full hematodochal inflation and deflation.

Procedures for Sperm Quantification.— The methods for sperm quantification are based on a modification of the protocol of Bukowski & Christenson (1997). Male palps were removed at the femur under a dissecting microscope. Right and left palps were then labeled and separated. Each palp was placed into a labeled 1.5-mL polypropylene centrifuge tube (Brinkman) containing 300 μL of a sonication solution of 1 mL of 0.9% saline and 10 μL of 10% Triton-X100 detergent

drawn from a common stock. Treatment with detergent was necessary to prevent sperm aggregation and facilitate a homogeneous distribution within a sample. Each palp was crushed with forceps and centrifuged at 1000 g for 5 min. After centrifugation, each sample was ultrasonicated using a Branson sonicator with a 3.2 mm probe at a low level (approximately 2% of total power output) for about 20 s. Exactly 300 µl additional sonication solution was added to the preparations that were then vortexed for approximately 10 s. A subset of the homogenized sample was immediately withdrawn and placed on a hemacytometer. Sperm were counted under a light microscope at 400× magnification. All values reported are estimates of total numbers of palp sperm based on linear extrapolations of actual counts to the total sample volume.

Estimating Sperm Release.—To estimate the amount of sperm available prior to mating, a subset of males were sacrificed and their sperm was counted (see below). The resulting average sperm count was used as an estimate of the amount of sperm available prior to copulation. Sperm release is calculated by subtracting the amount of sperm remaining in the palps after copulation from the amount of sperm available prior to copulation. This is a conservative estimate of sperm release for males used in the mating studies. A more accurate estimation would be to restrict all males in the mating studies to one palp insertion, and compare used and unused palps for each male to directly determine sperm release. However, limiting males to only one palp insertion would create other artifacts when examining the overall length of mating, so this method was only used for this subset of males.

To measure sperm release, a subset of virgin males were allowed to copulate and transfer sperm from only one palp to a virgin female before being sacrificed for sperm counting (i.e., half-virgin males). After the male completed his first palp insertion (i.e., removed the first palp and began to position his other palp for insertion), the male was immediately removed and placed at −80° C for sperm counting later. These males are described as "one-insertion" males. This allowed a direct comparison between the amount of sperm in the unused and used palps, i.e. the amount of sperm available prior to copulation and the amount released during

copulation, for each individual. The average sperm count of the unused virgin palps was used to estimate the amount of sperm available prior to copulation in the staged matings. The amount of sperm available prior to copulation for wild-caught adult males was unknown, as males may be sperm-depleted or have higher reserves from re-inducting sperm multiple times. To be conservative, calculations of sperm release from wild-caught adult males were based on the average sperm count of the unused palps of virgin laboratory-reared males. For comparison, several wild-caught males were allowed to mate using only one palp (in a similar fashion as above) to directly determine how much sperm was available before copulation and released during palp insertion for those particular males.

Statistical Analyses.—The Mann-Whitney U test was used to assess differences in the amount of palp sperm among and within virgin and mated males. The Kruskal-Wallis test was used for comparisons between males mated to virgin, non-virgin, and wild-caught females. Non-parametric Spearman rank correlation was used to test for associations between copulation duration and sperm release. All summary statistics of continuous variables are reported as $\bar{X} \pm$ SE.

RESULTS

Field Studies.—The following section describes the natural history of *G. emertoni*, including observations on mating behavior.

Habits: Overall, 112 adult, 40 penultimate-molt and 23 immature individuals were observed. During daylight hours, adult and penultimate individuals (respectively, $n = 69$, $n = 40$) were found near the stream under leaves, rocks or overhanging vegetation, whereas immatures ($n = 23$) were found in miniature webs suspended in between grass stems approximately three cm above the stream. When resting on vegetation (e.g., grass) diurnally, *G. emertoni* adopt a cryptic posture by extending leg pairs (1, 2) parallel to and wrapping leg pairs (3, 4) around a stem. Occasionally, adult females were found on the remnants of a web during the late afternoon on overcast days ($n = 7$), but were more often in their daytime retreats ($n = 19$). Retreats consisted of a few silk lines attached to the vegetation. Diurnally, adult and penultimate individuals were found in retreats (respective-

ly, $n = 43$, $n = 40$). After dusk, female adults were found on webs ($n = 27$) and male adults were either found moving between aggregations of females ($n = 5$) or resting beside a female's web ($n = 11$).

Adults were observed rebuilding their webs nightly. Typically, individuals emerged after dusk and began to spin webs three to five cm above the water surface. On multiple occasions, adult females built webs inside the webs of *Tetragnatha versicolor* (Walckenaer 1842), but no territorial aggressions between the two species were seen either during or after web construction.

Avoidance Behavior: When disturbed, *G. emertoni* dropped into the water beneath and traveled downstream, floating along with the current. To emerge from the water, they extended their legs, which retarded their downstream movement, and climbed up streamside vegetation. During collection, several *G. emertoni* traveled approximately one meter downstream on the current, but more escaped until an appropriate technique was developed: placing a mesh net underneath the individual as collection was attempted.

Mating Behavior: Three matings were observed in the field. Males approached females on webs ($n = 2$) or resting on vegetation ($n = 1$, this female left before sperm transfer and is excluded from analyses below, see Mate-Avoidance Behavior). Upon contact, adults immediately paired in a ventral-to-ventral mating position by interlocking their chelicerae. Then males began a vibratory courtship phase ($n = 2$, latency to courtship $\bar{X} = 11 \pm 6$ sec, courtship duration $\bar{X} = 123 \pm 37$ sec); this phase was considered courtship because it occurs before palp insertion and sperm transfer. During courtship the male rapidly flicked leg pairs (1, 2) over the female, until she exhibited an acceptance posture—curling her abdomen towards the male—a necessary step to bring her gonopore within reach of his palps.

In the field, a male inserted one palp, and then inserted the other palp, using each palp only once ($n = 2$, copulation duration $\bar{X} = 803 \pm 270$ sec). The insertion of pedipalps appears to be ipsilateral, but further confirmation of this would require freezing pairs *in copula* to determine the placement of the palp because the openings to the female spermathecae are located interior to the epigastric

fold and, therefore, are not visible during mating. The two complete matings observed in the field were shorter in duration ($n = 2$, total duration $\bar{X} = 936 \pm 240$ sec) than those observed in the laboratory.

Males left females immediately after mating in the field, suggesting that there is no post-copulatory mate guarding in this species. Yet, in the late spring when most of the matings were observed, females were rarely collected from their daytime retreats without at least one male nearby. More often, a female was collected from her retreat with two or three males nearby ($n = 11$, $n = 4$, respectively). Occasionally, an adult pair was collected with up to five males in the surrounding vegetation (within 10 cm of the pair, $n = 4$). It is unknown if males compete for access to females within these groups during the day (see Discussion).

Mate-Avoidance Behavior: On one occasion in the field, an unusual mate-avoidance behavior was observed between a pair of adults with interlocked chelicerae on a stem of grass overhanging the stream. The female appeared to be resisting copulation: she held her abdomen away from the male and began moving backwards, pulling the male down the stem towards the water. Once she made contact with the stream, she released her hold on the grass entirely and floated on the water, still held by the male's chelicerae interlocked with her own. Seconds later, after touching the female with leg pairs (1, 2), the male disengaged his chelicerae and during this momentary release the female was quickly pulled away by the current. Approximately one meter downstream, the female extended her legs to grasp another grass stem and emerged from the water. The male remained on the original grass stem, skimming leg pairs (1, 2) across the water surface for about 30 s before returning to a resting position higher up on the grass stem. Another example of this mate-avoidance behavior also occurred in the laboratory.

Egg Sacs: Egg sacs were between pairs of moist leaves stitched tightly together with silk located in streamside litter, just above the water line. The base of the egg sac was spun onto a leaf surface, eggs were deposited, and a second tightly woven sheet was placed over the eggs before being attached loosely to the other leaf. The egg sac was distinctly flattened, its upper surface being slightly concave. Two

Table 1.—Summary of mating behavior for laboratory-reared virgin males mated to virgin and non-virgin females, and wild-caught males mated to wild-caught females in the laboratory, $\bar{X} \pm SE$ (n).

	Female type		
	Virgin	Non-Virgin	Wild-Caught
Latency to courtship (s)	40 ± 7.6 (8)	42 ± 7.9 (8)	<1 (3)
Courtship duration (s)	126 ± 34 (8)	151 ± 14 (8)	110 ± 5 (3)
Copulation duration (s)	1,000 ± 180 (8)	700 ± 110 (8)	1,734 ± 400 (3)
Total duration (s)	1,250 ± 180 (8)	1,050 ± 160 (8)	2,035 ± 626 (3)

sacs were collected, each of which had 20–30 eggs inside. The egg sacs were fairly large (3–4 mm across) relative to the adult body size of *G. emertoni* (4.5–5 mm). In the lab, females laid multiple sacs (maximum = 4) ranging from 16 to 26 eggs per sac. The hatchlings had a well-developed stout cephalothorax and, upon casual visual inspection, appeared to be larger than hatchlings of *Tetragnatha versicolor* (Walckenaer 1842) and *Leucauge venusta* (Walckenaer 1842).

Laboratory Studies.—The following section describes the experimentation on mating behavior and sperm release.

Mating Behavior: In the laboratory, just as in the field, males and females interlocked chelicerae immediately upon contact and males began courtship less than a minute later (Table 1). Vibratory courtship consisted of the male flicking his legs (pairs 1, 2) dorsally over the female until she adopted an acceptance posture. The male then used his legs to move the female's abdomen closer, sometimes shaking her until he successfully inserted his first palp.

Upon insertion, the palp hematodochae inflated and deflated repeatedly. In the staged matings, both laboratory-reared virgin and wild-caught males alternated palps, and in most cases, inserted each palp only once before disengaging chelicerae. There were no significant differences in the number of palps used by virgin males when mating with virgin and non-virgin females (Fisher's exact test, P = 0.23), but two males mating non-virgin females did insert a palp twice. In each case, the palp inserted a second time was the one with the shortest initial insertion duration. These matings were otherwise as described above with cheliceral engagement lasting the duration of the mating. Out of 16 matings, two laboratory-reared males (not the same males from the previous case) briefly disengaged

their chelicerae after the first palp insertion and then immediately re-engaged chelicerae and re-courted the female before inserting the second palp. All wild-caught males inserted each palp only once. Sperm extrusion was not observed during or after any staged mating.

Mating propensity, latency to courtship, courtship duration, palp insertion duration, and overall mating duration were compared for all females. Laboratory-reared males were equally as likely to mate virgins as non-virgins (n = 18, χ^2 = 1.80, P = 0.18); ten virgin females were mated immediately by the first male presented to them and eight mated with the second male presented to them. (The two singly-mated females and their mates were excluded from the analyses.) Latency to courtship (after cheliceral engagement), was not significantly different for males courting virgin and non-virgin females, but was lengthier than that of wild-caught males (Mann-Whitney, U = 29, P = 0.75; Kruskal-Wallis, df = 2, H = 7.3, P = 0.03, respectively; Table 1). In contrast, the courtship duration was significantly longer for laboratory-reared males courting non-virgin than virgin females, but neither was significantly different from courtship of wild-caught males (Mann-Whitney, U = 13, P = 0.05; Kruskal-Wallis, df = 2, H = 5.3, P = 0.07, respectively; Table 1). When all palp insertions were considered jointly, insertion duration was not different between first and second laboratory-reared males although there was a trend for insertions with non-virgins to be shorter in duration (n = 16, virgin $\bar{X}$ = 503 ± 71; n = 16, non-virgin $\bar{X}$ = 348 ± 65; Mann-Whitney, U = 83, P = 0.14). When only first insertions were considered, males mated to non-virgin females had shorter insertions than those mated to virgin females (Mann-Whitney, U = 11, P = 0.05); however, when second insertions were compared, there was no difference (Mann-Whit-

Table 2.—Total sperm released and sperm remaining for both palps of virgin males mated to virgin and non-virgin females in the laboratory, $\bar{X} \pm$ SE (n). *To calculate release, the sperm retained in the mated palp was subtracted from the estimate of sperm available prior to copulation.

	Female type	
	Virgin	Non-Virgin
Sperm released*	710,000 ± 87,000 (8)	740,000 ± 87,000 (8)
Sperm remaining	300,000 ± 110,000 (8)	200,000 ± 78,000 (8)

ney, $U = 29$, $P = 0.79$; Table 1). Wild-caught males had lengthier palp insertions than laboratory-reared males (Kruskal-Wallis, $df = 2$, $H = 6.1$, $P = 0.05$; Table 1). There was no significant difference in total copulation duration between males mated to virgin and non-virgin females and those mated to wild-caught females (Mann-Whitney, $U = 22$, $P = 0.29$; Kruskal-Wallis, $df = 2$, $H = 3.1$, $P = 0.22$, respectively; Table 1); however, there was a trend for copulation to be shortest with non-virgin females and longest with wild-caught females. Wild-caught males observed in the laboratory had a total copulation duration that was longer, but not significantly so, than those observed in the field (Mann-Whitney, $U = 1$, $P = 0.25$; Table 1).

Mate-Avoidance Behavior: In one case, the female mate-avoidance behavior already noted in the field was seen again in the laboratory. During one staged mating between wild-caught spiders, after pairing and engaging chelicerae, the female began resisting sperm transfer. She kept her abdomen away from the male's palps and walked backwards down the branch towards the aquarium water. Upon contacting the water, the female released her hold on the branch and floated on the water surface next to the branch. Yet, perhaps because there was no current pulling her away, the male was able to keep his chelicerae interlocked with the female and continue courting. Courtship lasted one hour and 31 s, possibly another measure of female resistance as typical courtship duration was approximately three minutes. The male managed to insert only his right palp for 11 min, but did not release any sperm (as determined afterwards by comparing the sperm remaining in the used palp to that in the unused palp), which may indicate that a more cryptic form of female resistance exists (this male was excluded from

all mating behavior and sperm release analyses).

Sperm Release From Laboratory-Reared Males: All males released sperm ($n = 16$). Males mated to virgins and those mated to non-virgins (i.e., first and second males to mate) did not have any significant differences in the sperm remaining in their palps and, as a consequence, no difference in the sperm released to females (Mann-Whitney, sperm remaining $U = 20$, $P = 0.21$; sperm released $U = 25$, $P = 0.46$, respectively; Table 2). The sperm available prior to copulation was estimated from the average sperm count of palps from virgin laboratory-reared males. Although there were no differences in sperm release between males, there was variation in sperm release and palp use within a male. Most males released sperm from each palp and used both palps exactly once during mating ($n = 10/16$). Two males mating non-virgin females released sperm from both palps but inserted the first palp twice, after the insertion of the second palp ($n = 2/16$). Some males released sperm from only one palp ($n = 4/16$). These four males (three mated to virgin females, one mated to a non-virgin female) inserted the first palp only once during copulation. The sperm release by a male was not correlated with the overall duration of copulation (Spearman rank correlation, $rho = 0.250$, $Z = 0.97$, $P = 0.33$).

Sperm Release From "One-insertion" Males: To look at natural variation in sperm number as well as sperm release, a subset of virgin laboratory-reared males ($n = 3$) and wild-caught males ($n = 3$) were allowed to copulate with only one palp before being sacrificed for sperm counting. These males are described as "one-insertion" males. Unused palps from virgin laboratory-reared males contained significantly less sperm than unused palps from wild-caught males ($\bar{X} = 483,000$

Table 3.—Summary of palp insertion, sperm release, and sperm remaining for the first palp only for virgin males mated to virgin and non-virgin females, and wild-caught males mated to wild-caught females in the laboratory, $\bar{X} \pm$ SE (n). *To calculate release, the sperm retained in the mated palp was subtracted from the estimate of sperm available prior to copulation.

	Female type		
	Virgin	Non-Virgin	Wild-Caught
Palp insertion (s)	563 ± 49 (8)	294 ± 88 (8)	659 ± 86 (3)
Sperm released*	477,000 ± 12,000 (8)	456,000 ± 23,000 (8)	470,000 ± 9,000 (3)
Sperm remaining	19,000 ± 9,000 (8)	27,000 ± 23,000 (8)	14,000 ± 9,000 (3)

$\pm$ 129,000, $\bar{X}$ = 1,026,000 $\pm$ 240,000; Mann-Whitney, U = 9, P = 0.05). This subset of males did release fully from the palp used in mating, as the amount of palp sperm remaining was similar for virgin laboratory-reared and wild-caught males ($\bar{X}$ = 14,500 $\pm$ 9,000, $\bar{X}$ = 14,000 $\pm$ 9,000; Mann-Whitney, U = 4, P = 0.83).

Sperm Release from First Palp Insertion: First palp insertion duration and sperm release were compared for males mated to virgin, non-virgin and wild-caught females (Table 3). The duration of the first palp insertion was significantly shorter for males mated to non-virgin females than for males mated to either virgin or wild-caught females (Kruskal-Wallis, df = 2, H = 7.5, P = 0.03; Table 3). Using the conservative method, the sperm retained and the sperm released from the first palp was not significantly different for males mated to virgin, non-virgin and wild-caught females (Kruskal-Wallis, sperm retained, df = 2, H = 1.57, P = 0.46; sperm released, df = 2, H = 0.56, P = 0.76; Table 3). However, the calculated sperm release for wild-caught males would be twice as much if a less conservative estimate was used: taking the average wild-caught, rather than virgin sperm count, to approximate the amount of sperm available before copulation (resulting in wild-caught male sperm release of $\bar{X}$ = 998,000 $\pm$ 9,000 per palp, Kruskal-Wallis, df = 2, H = 7.3, P = 0.03; compare to Table 3). Two males did not release any sperm and so were not included in these statistical analyses (one male was mated to a non-virgin female, the other male was mated to a wild-caught female).

Sperm Release Patterns: I calculated the relative sperm release by the first and second laboratory-reared male for each doubly-mated female in the study. This calculation is useful to provide a null hypothesis for future tests of pa-

ternity patterns in this species. S_2 is the proportion of sperm from the second male to mate (S_2 = Sperm$_{2nd\ Male}$/Sperm$_{Total}$). Using the convention of Christenson & Cohn (1988), sperm release patterns were categorized as first-male biased ($S_2 \leq$ 0.33), mixed (S_2 = 0.33–0.66), and last-male biased ($S_2 \geq$ 0.66). Sperm release patterns were variable: mixed (n = 4), last-male biased (n = 3) and first-male biased (n = 1). Each case of bias, either first- or last-male, resulted from a male releasing sperm from only one palp whereas the other male released from both palps, possibly gaining an advantage in sperm competition. Overall, S_2 values averaged 0.51 $\pm$ 0.05 (n = 8).

DISCUSSION

Glenognatha emertoni are well-hidden in the daytime, and emerge at dusk to spin orb webs over the stream. Male *G. emertoni* do not cohabitate with or guard females on their orb-webs. Instead, males leave females immediately after mating, similar to *Tetragnatha* species (LeSar & Unzicker 1978; West & Toft 1999; Danielson-François 2002; Danielson-François & Bukowski 2005), but unlike pholcid species that commonly have cohabitation (Eberhard & Briceño 1983; Eberhard et al. 1993; Blanchong et al. 1995; Kaster & Jakob 1997). During the day, *G. emertoni* females are found in retreats, but not alone—typically more than one male is nearby. Some females had as many as five surrounding males, but whether this was due to chance, mate-guarding of or a male preference for particular females remains to be tested (c.f. Danielson-François et al. 2002).

Males do not appear to discriminate between virgin, non-virgin, and wild-caught females, being equally likely to court and mate each type of female. Despite this lack of discrimination, there were some differences in

mating behavior. Laboratory-reared males courted non-virgins significantly longer than virgin females, and wild-caught adult males tended to get to the courtship phase more quickly than laboratory-reared virgin males. *Glenognatha emertoni* mating behavior was unique in having a vibratory phase of courtship that was absent in its congeners, but otherwise was similar to that of other tetragnathines in using chelicerae as holdfasts during mating (Barrows 1919; LeSar & Unzicker 1978; Huber 1998; West & Toft 1999; Danielson-François 2002; Danielson-François & Bukowski 2005). After cheliceral engagement, latency to courtship was brief (less than one min) and vibratory courtship (leg-tapping) lasted several min. Overall mating duration with laboratory-reared males was approximately 20 min, similar to the 15 min observed for *G. foxi* (Barrows 1919). Wild caught-males mated in the laboratory had a 40 min duration, whereas those observed in the field had a shorter duration, about 17 min.

Consistent with the lack of overt discrimination between females based on mating history, *G. emertoni* males released equivalent amounts of sperm to virgin, non-virgin, and wild-caught females. This pattern of sperm release was also noted in the related haplogyne *Tetragnatha versicolor* Walckenaer 1842 (Danielson-François & Bukowski 2005), but was distinctly different from the sperm release pattern of the related entelegyne orb-weaver *Nephila clavipes* (Linnaeus 1767), whose males preferentially release sperm to virgin females, but release none, or only a greatly reduced amount, during mating to non-virgin females (Christenson & Cohn 1988).

Despite a lack of significant differences in sperm release to virgin and non-virgin females, there was variation among *G. emertoni* males in sperm release. Calculated for each doubly-mated female in the study, the resulting proportion of sperm released by the second male to mate resulted in a range of first-to last-male bias (0.33–0.68), and yielded an average sperm release of 0.51 ± 0.05, similar to that observed for *T. versicolor* (Danielson-François & Bukowski 2005). First and second males typically released sperm from both palps, and all males inserted both palps at least once during mating, but sometimes a male would release sperm from only one of his palps and not the other, resulting in a bias in sperm release. Whether releasing sperm from only one palp during mating was due to cryptic actions by the male or female remains to be seen.

Huber & Eberhard (1997) suggest that haplogyne males might be able to influence paternity by repositioning rival males' sperm due to the short insemination duct found in most haplogyne taxa. In the haplogynes *Physocyclus globosus* and *Leucauge mariana* (Taczanowski 1881), males had extensive palpal movements that differed for virgin and non-virgin females (Huber & Eberhard 1997; Eberhard & Huber 1998). In the haplogyne *Pholcus phalangioides*, second males gain higher paternity even though they copulate for a shorter amount of time than first males (Yoward 1998). A detailed examination of *P. phalangioides* revealed that paternity was influenced by the number of pedipalp movements made by the second male, and Schäfer & Uhl (2002) suggest that these movements could remove rival's sperm. Consistent with the above studies, the flexible and short common insemination duct in *G. emertoni* would seem to make them particularly susceptible to this sort of manipulation (Danielson-François 2002).

The short and flexible nature of the haplogyne insemination duct may also increase the evolutionary lability of palp insertion patterns. Huber & Senglet (1997) argued that the absence of a "lock-and-key" fit between male and female genitalia in taxa within the entelegyne family Tetragnathidae made it possible to switch from the usual ipsi- to contra-lateral insertion, inserting the right palp into the left side of the epigynum. In contrast to the rest of the tetragnathine genera (i.e., *Tetragnatha* and *Pachygnatha*) and *Leucauge*, *G. emertoni* insertion patterns appear to be ipsilateral. Similarly, *G. heleios* also has an ipsilateral palp insertion pattern (Edwards & Senske 2001). The palp insertion patterns of *G. emertoni* were based on behavioral observations. Further confirmation of this result would require examination of pairs flash-frozen *in copula* (c.f. Huber & Senglet 1997) to physically determine which side (right or left) the palp enters.

Female *G. emertoni* appear to have a suite of resistance behaviors, one of which may have its origins in a startle behavior common to both sexes—dropping out of the web and

into the water below. The floating ability of spiders is influenced, in part, by the hydrophobicity of the cuticle and the density of hairs (Suter et al. 2004). Although the hydrophobicity of cuticle in *G. emertoni* is unknown, this small spider has a dense set of hairs covering the body that may aid its ability to float. Dropping into the current and floating downstream may prove to be a common mode of transport once more species are examined, but currently there is less information on floating as a means of travel even though locomotion across the water surface (e.g., walking, rowing, and galloping) is a well-documented phenomenon in spiders (Suter et al. 2003; Stratton et al. 2004).

Eberhard (2004) suggested that spiders are excellent organisms for the study of sexual selection, and in particular sperm competition. As a general method, examining the amount of sperm released per male during mating can be used to generate a null hypothesis for testing the mechanisms underlying paternity patterns in spiders. One such null hypothesis would be that the proportion of sperm from the second male to mate, S_2, would be equivalent to—under a simplistic "lottery" model (Parker 1998)—the expected paternity for the second male (P_2, *sensu* Boorman & Parker 1976). This is a null hypothesis that can and should be explicitly tested in future paternity studies. Given the pattern of sperm release found in *G. emertoni*, the null hypothesis based only on sperm release would be mixed paternity, all else being equal. The relationship of sperm release to paternity patterns has yet to be studied for *G. emertoni*, and if male or female manipulation of sperm release and storage occurs, it is unlikely that such a simplistic scenario will hold. Future work is needed to determine the actual paternity pattern by obtaining empirical P_2-values and comparing them to sperm release within the same study.

In summary, *Glenognatha emertoni* mating behavior was fairly simple, with a short latency to copulation and a phase of vibratory courtship before a single palp insertion (ipsilateral) from each palp (right and left) to transfer sperm. Males left immediately after copulation and did not cohabitate with females on their orb webs. Males released equivalent amounts of sperm to females, regardless of their mating history, similar to the only other haplogyne studied for sperm release behavior.

Females actively resisted courting males by releasing from them and floating downstream, and may have a cryptic method of preventing sperm release during copulation. Future studies will examine the relationship among sperm release, mating behavior, and paternity patterns in *G. emertoni* and other haplogyne species.

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SOCIAL BEHAVIOR IN AMBLYPYGIDS, AND A REASSESSMENT OF ARACHNID SOCIAL PATTERNS

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ABSTRACT. Aggregation, extended mother-offspring-sibling interactions, and complex social behaviors are extremely rare among arachnids. We report and quantify for the first time in Amblypygi prolonged mother-offspring-sibling associations, active aggregation, and frequent "amicable" (tolerant, nonaggressive) tactile interactions in two species: *Phrynus marginemaculatus* C.L. Koch 1840 (Phrynidae) and *Damon diadema* (Simon, 1876) (Phrynichidae). Sociality is characterized by frequent contact and tolerance, and infrequent agonism until sexual maturity in *D. diadema* and into adulthood in *P. marginemaculatus*. We experimentally examined potential benefits and costs affecting aggregation: risk of predation, preferred habitats and prey availability. Only increased predation risk decreased nearest-neighbor distances and increased maternal vigilance. Individuals aggregated on a variety of surface textures and locations that varied daily, rather than aggregating only on preferred microhabitats. Manipulation of prey abundance had no affect on the tendency to aggregate.

Patterns of parental care, duration of association, and the presence of social traits found in the most social taxa of non-spider arachnids are reviewed. Species in most arachnid orders have transient parental care with defense of eggs, a brief period of association with newly emerged young prior to independent foraging and explosive dispersal from the natal nest. More prolonged sociality, with long-term associations among mothers-offspring-siblings is rare and is only described in a few species in the Amblypygi, Scorpionida, Pseudoscorpionida, and Acari. All such species have subsocial origins, but current use of the term subsocial is overly broad and we propose a more restricted terminology for clarity.

Keywords: Whip spiders, aggregation, maternal care, ontogeny, predation risk, foraging

Sociality in arachnids is extremely rare. Here we report prolonged association between mothers and their immature offspring, active aggregation among siblings, and extensive social contact in two species of captive amblypygids, *Phrynus marginemaculatus* C.L. Koch 1840 (Phrynidae Blanchard) and *Damon diadema* (Simon 1876) (Family Phrynichidae), that differs from the solitary behavior previously described for amblypygid adults. Subsociality, or an association between mothers and their offspring or among siblings prior to reaching sexual maturity, has not been previously reported in the Amblypygi. Although arachnid sociality at all levels of complexity is uncommon, sociality has been applied to describe behaviors ranging from transient early parental care (Laniatores opilionids: Machado & Raimundo 2001; Machado 2002; Uropygids: Schmidt 2003), to "subsocial"

mother-offspring-sibling associations that last for brief periods (spiders: Kim 2000; Schneider 1995; scorpions: Polis & Lourenco 1986), "subsocial" associations that last until sexual maturity (spider mites: Saito 1997; Mori & Saito 2005; amblypygids: this manuscript), to the complex multiple adult societies of the most social of the colonial and cooperative spiders (reviews in Buskirk 1981; Aviles 1997; Whitehouse & Lubin 2005) (see Tables 1–3 for details). Along with describing patterns of social interactions in amblypygids, we propose expanding and modernizing the definitions of subsociality to better interpret the social and evolutionary implications that allow these rare predatory species to successfully live in groups.

Beyond studies of the dramatic courtship and fighting behavior of adult amblypygids (Alexander 1962; Weygoldt & Hoffman 1995; Weygoldt 2000, 2002) relatively little work has been done on other aspects of amblypygid behavior. Most studies suggest that adult amblypygids are generally solitary and intolerant

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Table 1.—General patterns of early parental care for each arachnid order. Due to a lack of information, Palpigradi and Ricinulei were excluded. Where informative, T indicates the pattern is typical for the members of the order, C indicates that this is common among some Families, and R indicates that only a few rare species exhibit the alternate pattern. Numbers refer to citations in all three Tables: 1 = Avilés 1997; 2 = Brach 1978; 3 = Buskirk 1981; 4 = Cloudsley-Thompson 1977; 5 = Coddington et al. 1990; 6 = Evans 1998; 7 = Harvey 2003; 8 = Kim 2000; 9 = Kullmann 1972; 10 = Machado 2002; 11 Machado & Oliveira 1998; 12 = Machado & Raimundo 2001; 13 = Machado & Vasconcelos 1998; 14 = Mahsberg 2001; 15 = Mori & Saito 2005; 16 = Polis & Lourenco 1986; 17 = Polis & Sissom 1990; 18 = Punzo 1998; 19 = Ramachandra & Bali 1990; 20 = Rowland 1972; 21 = Rayor & Taylor 2006;

Parental trait	Arachnid order			
	Araneae	Amblypygi	Uropygi	Schizomida
Carry egg sac	C	T: 28	T: 19, 23	20
Live young				
Guard eggs	C			
Youngest instar carried	R	T: 28	T: 23	20
First mobile instar guarded	C	21	23	
No Association with 1st instar	C			
Association with 1–2 instars prior to explosive dispersal	R	T: 28	19, 23	7, 20

predators. No work has evaluated whether these traits are also characteristic of juvenile and subadult amblypygids. According to Weygoldt (2000) "Whip spiders are not social animals, in fact they are not even gregarious. On the contrary, they avoid each other or react aggressively when encountering a congener." Other researchers have also concluded that adult amblypygids are solitary animals both in the field and laboratory (Gray & Robinson 1986; Alexander 1962). Alexander (1962) observed only aggressive and threatening behavior between adult conspecifics of both sexes in *Damon variegatus* (Perty 1834; from central and southern Africa) and *Phrynus barbadensis* (called *Admetus barbadensis*) (Pocock 1894; from Barbados). She concludes that much of the intraspecific behavior that does not lead up to courtship "consists of threatening contests in which the delicate feelers [whips] are used as 'weapons'." Other accounts describe similar adult male-male conflicts (Weygoldt & Hoffman 1995; Weygoldt 2000).

In contrast, Weygoldt (1977) found that *Heterophrynus longicornis* Butler 1873 (Family Heterophrynidae) from the Brazilian Amazon were especially tolerant of one another. Individuals were often found in male-female pairs, along with a variable number of immature individuals, up until the fourth or fifth instar. In one case seven adults were found inhabiting a large log. Quintero (1981) notes

that "Within favorable habitats, [*Phrynus asperatipes* Wood 1983, from Mexico] individuals tend to aggregate, and numerous specimens could be collected from a single cave." It is common in outhouses or slit latrines throughout the neotropics, to find multiple amblypygids in proximity to one another, probably to take advantage of the abundant insect prey at such sites (Rayor pers. obs.). In Florida, *P. marginemaculatus* are frequently associated with lightning downed trees with active termite colonies where a number of amblypygids may be found approximately 30 cm apart at regular intervals along the termite trails (T. Gearheart pers. comm).

Female amblypygids lay eggs and carry them in a brood pouch underneath their abdomen and the newly emerged young climb onto their mother's abdomen for the duration of their first instar (first incomplete juvenile or pullius, Canard & Stockmann 1993; praenymphae, Weygoldt 2000). Alexander (1962), Weygoldt (2000), and we have observed that if one of the immobile, helpless young falls from the mother's back during the first instar, and cannot get back on, the mother will do nothing to help, and may even eat this individual. From observations of this behavior, Alexander (1962) concludes "that there is no maternal behavior towards young [amblypygids] that leave their perches on the back of the mother" (Alexander 1962). However, Mahsberg (2001) describes similar cannibal-

Table 1.—Extended. 22 = Saito 1997; 23 = Schmidt 2003; 24 = Schneider 1995; 25 = Shivashankar 1994; 26 = Tizo-Pedroso & Del-Claro 2005; 27 = Weygoldt 1969; 28 = Weygoldt 2000; 29 = Whitehouse & Lubin 2005; 30 = Zeh & Zeh 1990. Note: There is extensive confusion over the different developmental patterns and terminology related to arachnid development (Canard & Stockmann 1993). In the arachnids, after emergence from the egg, in most there is a first instar (incomplete juvenile) that does not feed independently and is essentially immobile, while the second instar is capable of feeding independently and is mobile. For each order, we have consistently referenced the patterns of behavior from the first mobile, independent instar as defined by Canard & Stockmann (1993).

Arachind order				
Opiliones	Solifugae	Pseudoscorpiones	Scorpiones	Acari
	C: 18	T: 26, 27		
			T: 17	
R: 12				R: 15, 22
		27	T: 17	
R: 12			17	R: 15, 22
T: 12	T: 4, 18			
R: 12	R: 4	T: 2, 26, 27, 30	T: 14, 17	R: 22

ism of first instars that have fallen from the mother's abdomen among the social emperor scorpions, *Pandinus imperator* Koch 1841, and suggests that maternal cannibalism at this stage weeds out deformed individuals in order to allocate energy towards other young with superior reproductive value. We consider Alexander's (1962) conclusions about the limits of maternal behavior based solely on damaged individuals during the first instar that cannot survive independently to be flawed.

Alexander (1962) concluded that after leaving their mother's back, young amblypygids were "clearly independent" of their mother. Gray & Robinson (1986) describe laboratory observations of a small Australian species, *Charinus pescotti* Dunn, 1949, that also disperse from the mother after undergoing their first molt. Weygoldt (2000) states that after the young leave the mother's abdomen (in a laboratory setting) they "begin their life without any further maternal care." However Weygoldt (2000) indicates that "in most species the nymphal instars are not aggressive towards each other; moreover, the mother is not aggressive towards her offspring. Growing animals become increasingly aggressive shortly before reaching maturity but the adults are more tolerant of each other."

In this paper, we expand upon Weygoldt's (2000) observations and describe in detail prolonged mother-offspring-sibling associations in two species of captive amblypygids, as well as associations between adults in one of these species. Our preliminary observations of *P. marginemaculatus* and *D. diadema* suggested that these animals not only tolerated one another, but consistently aggregated and interacted frequently with extensive whip contact. Here we document the tendency to aggregate, how social dynamics change with maturity, and the role of the whips in mediating social contact among amblypygids. In addition, we investigated the following three questions to evaluate possible costs and benefits that individuals may experience by aggregating. First, do individuals form aggregations merely to gain access to particularly favorable microclimates within our experimental cages? Second, given that amblypygids are obligate predators that potentially compete for prey (Weygoldt 2000), do differences in prey abundance effect individuals' tendency to aggregate? Third, since aggregation is often associated with reduced risk of predation (Alexander 1974), does the presence of a potential predator or a disturbance affect group size or proximity to other members of the group? Finally, we review the patterns of early parental care and more complex social behavior known for each of the non-Araneae arachnid orders, and make proposals about characterizing social behavior in these species.

METHODS

Study animals.—Two species of amblypygids were used in this study. Male, female, and

Table 2.—Patterns of association in the most social species known for each arachnid order. Citations are given as in Table 1. The numbers of species (*n*) known to display this type of association are listed for the non-Araneae arachnids. Spiders are represented by a few token species that represent particular features. The Acari are only represented by the seven tetranychid spider mites whose patterns of association

Social trait	Arachnid order			
	Araneae	Amblypygi	Uropygi	Schizomida
Association past 2nd instar, for 1–2 additional instars	8, 29			
Association part-way through development	3, 24			
Association up to sexual maturity	6	Dd, 21; *n* = 1		
Associate past sexual maturity-multiple adults	1, 29	Pm, 21; *n* = 1		

spermatophore stalk voucher specimens of *D. diadema* have been deposited in the Cornell University Insect Collection and at the Smithsonian National Museum of Natural History. Voucher specimens of *P. marginemaculatus* have been deposited in the Cornell University Insect Collection. Extensive video documentation of both species' social interactions and the exploratory response to lizards are available through the Cornell Laboratory of Ornithology, Macaulay Library. Video vouchers are archived in the Macaulay Library and can be found at: http://animalbehaviorarchive.org (or from the author). These videos can be located through an Advanced Search of the Notes for "Rayor Amblypygid Sociality" or "Rayor amblypygid predator exploration" or by species name, Rayor, & behavior.

P. marginemaculatus (Phrynidae) is a small species common in southern Florida, often found on houses, under boards, logs, trash, under the bark of dead trees, and limestone outcrops (Muma 1967, Hebets pers. comm.). All specimens used in this study were collected from pine and oak flatlands near Fort Myers, FL by Todd Gearheart between January 1998 and August 2000. Interactions between *P. marginemaculatus* mothers and offspring were observed in two clutches from emergence through eight months. Adult spatial interactions were observed in a captive colony of 29 unrelated adult and subadult *P. marginemaculatus*.

The second species, *D. diadema* (Phrynichidae), is found in coastal forests and caves in Tanzania and Kenya (Weygoldt 1999). Adult specimens were caught in southern Tanzania near the Usubara Mountain Range by local collectors and sold for export (Somma & Gearheart, pers. comm.), and all young were born in captivity. Body sizes of *D. dia-*

dema closely match the allometric changes in body and palp width reported by Weygoldt (1999). Mother-offspring-sibling interactions in *D. diadema* were observed in five clutches produced by three adult females. Here we report spatial and behavioral changes that occurred during the first year until sexual maturity for the five groups, but most of the experimental data reported in this paper were collected from Group 4 (see Group details below). Spatial dynamics were observed in a group of ten unrelated adult *D. diadema*.

In total, nine amblypygid groups of different ages and housing conditions were observed. Initial clutch or group size is given for each group. All ages for immatures relate to the start of the second instar when the young descended from the mother's abdomen and were independently mobile and are referred to as the "emergence date." The emergence date at the start of the second instar is comparable to the point when young, newly mobile uropygids and scorpions descend from their mother's back. The groups were: Group 1 (clutch size *n* = 12) and Group 2 (*n* = 18) each consisted of a single *P. marginemaculatus* mother and her offspring (emergence in late August 1998; observed September 1998–April 1999). Group 3 was a mixed colony of unrelated young, subadults and adults of *P. marginemaculatus* (group size *n* = 29: females = 13, males = 8, undetermined sex = 7; observed August 2000–May 2001). Group 4 consisted of one *D. diadema* mother and her offspring (clutch size *n* = 18; emergence November 1999; observed November 1999–March 2001). Groups 5–8 each consisted of *D. diadema* mothers housed with their offspring from May 2001 through October 2002. Group 5 (*n* = 32; emergence 24 April 2001) and Group 6 (*n* = 38; emergence 24 May

Table 2.—Extended. have been well studied, and omit species whose social interactions are anecdotal (Saito, pers. comm.). For the amblypygids, we have indicated the categories in which *Damon diadema* (Dd) and *Phrynus marginemaculus* (Pm) fit into the scheme based on the data in this paper.

| Arachnid order | | | | |
Opiliones	Solifugae	Pseudoscorpiones	Scorpiones	Acari
			14; $n = 8$	22
			14, 25; $n = 1$	15, 22; $n = 3$
			14, 16	22
		2, 26, 30; $n = 3$	16; $n = 2$	22; $n = 4$

2001; same mother as Group 4). Group 7 (n = 50; emergence 18 November 2001). Group 8 (n = 20; emergence 28 April 2002) born to the Group 5 female, and resided with their mother and subadult Group 5 siblings. Group 9 consisted of unrelated mature adults of *D. diadema* (n = 9: 6 females, 3 males; observed from August 2000–February 2001). When two females in a group oviposited, they were removed from the group cage.

Housing and Diet.—All animals were housed in clear plastic or glass aquarium cages with a substrate of vermiculite and potting soil to maintain humidity. Cage sizes for *P. marginemaculatus* were: Groups 1 and 2—10 × 10 × 18 cm; Group 3—50 × 25 × 30 cm. Cage sizes for *D. diadema* were: Groups 4 and 6—50 × 25 × 30 cm; Groups 5, 7, and 9—50 × 26 × 42 cm. Large sheets of cork bark were tilted along the vertical glass walls of each cage to provide a climbing surface with easy observer visibility. *P. marginemaculatus* were strongly thigmotactic and preferred to rest in the tight space between two vertical surfaces, in this case, the space between the glass walls of the cage and the surface of the cork bark. *D. diadema* were less thigmotactic but also favored the vertical surfaces between the glass walls and the cork bark. In all cases, the cages and sheets of bark were sufficiently large that all individuals could distribute themselves far apart from other individuals within the cage on suitable habitat. All animals were fed appropriate sized crickets (*Acheta domesticus, Gryllus bimaculata* or *G. oceanicus*) *ad lib* several times per week (except during periods of experimental manipulation of their diet). All cages were placed on turntables, so that they could be rotated and individuals in all positions in the cages could be viewed with minimal disruption. Because of the regular rotation of cages, all positions

within the cages were presumed to have equal exposure to light or to human activities within the room. Behavioral and spatial observations were made at various times throughout the day and night, typically in the dark under red light. Additional behavioral observations were recorded in almost total darkness using a Sony digital camcorder (model DV-TRV9), with "nightshot" infrared lighting.

Amblypygid Whips.—The sensory and social lives of amblypygids are clearly centered on the first pair of legs (or whips), which are extensively used for odor discrimination (Hebets & Chapman 2000), spatial location, and tactile contact between individuals (personal observation). The whips are modified into thin antenniform sensory structures that can measure three to six times the length of the body. The whips are covered with sensitive chemosensory and mechanosensory setae (Foelix et al. 1975; Foelix & Hebets 2001; Foelix et al. 2002), and are capable of extremely delicate movements approximately 340° around the axis of their bodies (pers. obs.). Whip contact among individuals was a characteristic aspect of amblypygid behavior in aggregations. It was not always possible to discern whether the whips actually made contact or simply passed within millimeters of each other—both were considered to be contact. Social interactions appear to be mediated through whip contact. Unlike the extremely rapid, directed flicking motions with a vertical component that characterize whip movements in aggressive interactions, particularly in intrasexual conflicts (see Weygoldt 2000, 2002), the whip movements involved in amicable social interactions were typically long, comparatively slow repeated movements of one individual's whips down the length of the others whip on a primarily horizontal plane. Throughout this research, we considered "within whip length"

Table 3.—Characteristic traits of the social arachnid species. Citations are as in Table 1. The occurrence of features that have been used to characterize sociality are identified for the social species indicated in Table 2. For the amblypygids, we have indicated the categories in which *Damon diadema* (Dd) and *Phrynus marginemaculatus* (Pm) fit into the scheme based on the data in this paper.

Social trait	Arachnid order								
	Araneae	Amblypygi	Uropygi	Schizomida	Opiliones	Solifugae	Pseudoscorpiones	Scorpiones	Acari
Tolerance of group members	1, 3, 9	Dd, Pm, 21			5, 10, 13		2, 26, 30	14, 16, 25	15, 22
Tendency to aggregate	1, 3, 9	Dd, Pm, 21					2, 26, 30	14, 16, 25	15, 22
Overlapping generations of kin	1	Dd, Pm, 21					2, 26, 30	14, 16, 25	15, 22
Prey sharing	29						2, 26, 30	14, 16, 25	
Cooperative construction or use of retreat	1						26	14, 16, 25	15, 22
Non-agonistic communicative behavior		Dd, Pm, 21					2, 26, 30	14, 16, 25	15, 22
Cooperative defense							2, 30	14, 16	15, 22
Temporary aggregations of adults and subadults	29				5, 10, 13		27	16	

to be an appropriate variable for evaluating whether the individuals were close enough to make contact with one another, and essentially, as a measure of tolerance between neighbors. As illustrated by Figures 3–8, amblypygids within whip length of one another were often far closer together and touching more body parts than simply their whips. "Whip length" was defined as the length of a single whip fully extended. Whips were measured from living animals through the glass sides of their cages as they extended their whips using dial calipers or retroactively measured from exuviae from marked individuals. Both methods produced comparable measures.

Mother-Offspring-Sibling Interactions.— To determine if mother-offspring and sibling spatial dynamics in *P. marginemaculatus* (Groups 1 and 2) and *D. diadema* (Groups 4–8) changed over developmental time, we recorded the locations of all individuals in the groups relative to one another in a scan sample taken no more than once daily at a randomly chosen point in time. At each scan sampling, we recorded how many young were found in mother-offspring groups, sibling groups, or solitarily. Individuals were considered to be within a mother-offspring group if they were within the mother's whip length, in a sibling group if they were within whip length of one or more other individuals, or solitary if they were beyond whip length of another individual. In *P. marginemaculatus*, both clutches were observed once to three times a week from the time they emerged though 4 months old (Total sessions when spatial data collected: Group 1, $n = 14$; Group 2, $n = 27$), with casual observations until they were 8 months old. In *D. diadema*, we also recorded each individual's location and nearest neighbor distance several times a week from emergence throughout the observation periods for Groups 4–7 (Total sessions when spatial data collected: Group 4, $n = 68$; Group 5, $n = 41$; Group 6, $n = 42$; Group 7, $n = 26$). Comparable spatial data were collected for adult *D. diadema* in Group 9 (Total sessions when spatial data collected: $n = 32$).

As preliminary observations suggested that young *P. marginemaculatus* oriented their bodies toward the mother, the angle of orientation of the young was calculated relative to the mother. During each scan sample to assess spatial dynamics, the spatial orientation of the

individuals toward one another was sketched at one randomly chosen time. Orientation was determined by measuring the vector angle between the direction of the young (the orientation of the midsagittal plane extended anteriorly through the longitudinal body axis toward the palps) and a line drawn toward the closest part of the mother's body using a protractor. The mean vector angle of orientation towards each adult female was calculated using the Rayleigh test (Batschelet 1981).

Whip contact among individuals was a characteristic aspect of amblypygid behavior in aggregations. If social interactions are mediated by whip contact, we would expect individuals to position themselves closer than one extended whip-distance apart. To evaluate this, we compared mean whip length for amblypygids of a given age with mean nearest neighbor distance at that age for *D. diadema* using *t*-tests. Whip lengths were measured directly with dial calipers and nearest neighbor distances were measured with a ruler through the glass walls of the observation cage, or distances were calculated from x-y coordinates.

In addition to the spatial data collected, extensive behavioral observations were made throughout their lives. Observations and records were made through direct observation and by video, in order to gain a better understanding of general behavior patterns of the amblypygids. These qualitative descriptions are reported where relevant.

Adult Dynamics.—Spatial data, including group association, nearest neighbor distances, whip length, and whether the animals were courting, were collected over time on the unrelated *D. diadema* adults in Group 9 for comparison with immature individuals.

Evidence of Aggregation in Immatures.—To determine whether there was evidence of aggregation by *D. diadema* (Group 4 at 10 months old), we recorded the locations of individuals on the cork bark within the cages once daily at one randomly chosen point in time for 19 days. We predicted that if individuals were evenly spaced throughout the cage or distributed at random, the number of individuals found on each piece of bark at a given time should be proportional to the area of that piece of bark. Since thigmotactic individuals preferred to rest in the vertical space between the bark and the glass walls of the cage, we used only the area on this side of the bark in

our calculations. Amblypygids do not have scopula and were unable to climb on the sides of the glass or plastic cages, so this area was not considered to be part of the potential usable space. We calculated the expected number of individuals for each piece of bark, based on the size following the logic above, and then used chi-square goodness of fit tests to evaluate whether the amblypygids were randomly or evenly distributed on the bark or whether there was evidence of aggregation.

Costs and Benefits of Aggregation.—*Manipulation of Spatial and Textural Uniformity:* To determine whether individuals aggregated to gain access to the most favorable or protected locations in the cages, we created an environment in which all surfaces were presumed to be texturally and spatially uniform by manipulating bark texture and unifying the position of the bark relative to the glass sides of the cages. Both *P. marginemaculatus* (Group 3) and *D. diadema* (Group 4 at 14 months old) were tested in "uniform" environments. The original cork bark was removed and replaced with uniform rectangular pieces of plywood (5 mm thick) approximately the same size as the four walls of the cage. The plywood was placed 2 cm from and parallel to the walls, so that every position in the cage was equally favorable in terms of texture, distance from the cage wall, and relative light levels. With the "uniform" plywood set-up, location and distance between individuals were recorded. To evaluate the animals' spatial distribution, the total area of the plywood was visually divided into rectangular areas of comparable size. If the animals were distributed at random, the expected number of individuals found in each of these areas of the plywood would be proportional to the size of that area. In Group 3 (*P. marginemaculatus*), the total area of the plywood was divided into 12 sections of equal area. In Group 4 (*D. diadema*), where the individuals were significantly larger and typically formed larger aggregations, the total area was divided into six sections of equal area. Chi-square goodness of fit tests were used to determine if individuals were randomly or evenly distributed or if there was evidence of aggregation.

Manipulation of Food Abundance: To determine if aggregation might increase the competition for food, we manipulated food abundance for the adult *P. marginemaculatus*.

For this experiment, Group 3 ($n = 29$) was divided up into two equivalent groups, and housed in separate 3.8-l glass cages. From 15 September through 22 October 2000, Group 3A ($n = 15$) was fed daily so that there were always at least ten live uneaten crickets in the cage at any given time. Group 3B ($n = 14$) was deprived of food during this time: only two small crickets were put into the cage at the beginning of each week of this period. From 25 October through 20 November, the feeding schedules were reversed so that Group 3A was food deprived and Group 3B was well fed. Observations were made several times per week ($n = 20$ observations) and both location and distances between individuals were recorded. For each individual, the linear distance to the nearest neighbor was determined on each observation day. The mean nearest-neighbor distance was then calculated for each individual during each experimental period and a paired t-test was used to compare these variables during the food deprived and the food surplus phases of the experiment.

Response to Disturbance and to a Potential Predator: Since reduced predation risk is one of the predicted benefits of sociality for most animals (Alexander 1974; Krause & Ruxton 2002), we predicted that young amblypygids would benefit by the presence of their mother or other amblypygids through active defense, earlier warning, or through aggregation. To determine the response of amblypygids to potentially dangerous disturbances or predators, we conducted two experiments. In the first experiment, we examined the response of a mother and her offspring to a disturbance in which the experimental cage was gently rattled for approximately 15 seconds. We recorded the siblings nearest neighbor distances and group size for two clutches of *D. diadema* (Groups 5 and 6) 5 minutes before the disturbance and then again 2 minutes after it. Disturbance trial replicates were done one or more days apart between. Data were collected for Group 6 at 1.5 and 8 months ($n = 4$ replicates at each age), and Group 5 at 2 months ($n = 4$ replicates). The data were analyzed using a mixed model with age group (3 age levels) and treatment (before and after the disturbance) as fixed effects and replicate for each group as a random effect, followed by a multiple comparison analysis using the Tukey-Kramer adjustment.

Little is known about the predators of amblypygids (Weygoldt 2000; Hebets 2002). As a first attempt to see if there is a reaction to an animal that could potentially be a predator, we introduced a generalist insectivorous, semi-arboreal, male lizard (*Anolis carolinensis*) as a potential predator into the cages of Groups 3, 4, and 7 in a second experiment. The interactions between the lizard and amblypygids were observed and videotaped for 1 hour in each cage before the lizard was removed. This lizard species is sympatric with *Phrynus*, and similar in size to insectivorous chameleons, gekkos, skinks, or agamid lizards which may prey on *D. diadema* in Tanzania (where our adult specimens were collected) (Conant & Collins 1998; Spawls 2002). The lizard measured 16.1 cm from nose to tip of tail, while the amblypygids ranged in size from the smallest specimens of *P. marginemaculatus* (body length = 6 mm) to the largest adult specimens of *D. diadema* (body length = 42 mm). Although the lizard may have had difficulty in killing the largest of the *D. diadema* adults, its size would have been sufficient for it to easily attack juvenile *D. diadema* or any of the *P. marginemaculatus*.

RESULTS

Mother-Offspring-Sibling Interactions.— From emergence through four months, more young *P. marginemaculatus* were found aggregated near their mother or in several groups of closely associated siblings than were found solitarily (Figs. 1–4). Patterns of association changed little during those first four months.

Young *P. marginemaculatus* in proximity to their mothers oriented their bodies towards her body significantly more than expected (Rayleigh test: Group 1: $r = 0.5704$, angle = 58.5, $P < 0.001$, $n = 67$; Group 2: $r = 0.3672$, angle = 49.6°, $P < 0.003$, $n = 69$). Such orientation indicates that the young are attentive to the presence of their mother. Similar directed orientation is seen in courting adults (Weygoldt 2000).

Our observation of these clutches of *P. marginemaculatus* young did not extend until they reached sexual maturity due to mass mortality from mites at nine months. We believe that *P. marginemaculatus* reach sexual maturity at between 12 to 18 months old. We have casual, unquantified observations of two ad-
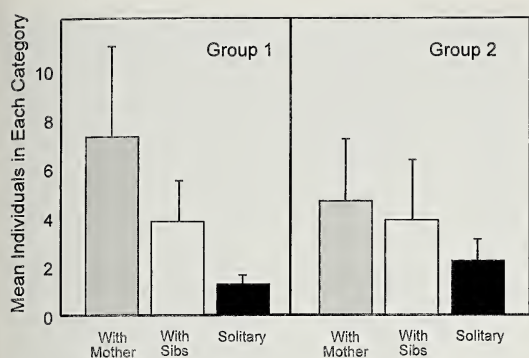
Figure 1.—Mean number (+SD) of *Phrynus marginemaculatus* young in Groups 1 and 2 found in association with their mother, in sibling groups, or solitarily. Data from Group 1 ($n = 14$ observations) and Group 2 ($n = 26$ observations) were collected on an approximately weekly basis from age 1 month to 4 months.

ditional clutches suggesting that when young are born into group colonies with multiple adults present, the young were not harmed and readily interacted with other adults. However, in both colonies mother-offspring groups were more labile than in the solo cages. Soon after the young emerged, the mother moved away from her offspring, while the young dispersed from the natal site in small groups to associate with older individuals throughout the colony.

Mothers of both species studied interacted frequently with their offspring; often the mother would sit in the middle of a group of her offspring and stroke their bodies with her whips. The following is a typical observation of *P. marginemaculatus* with three-week-old young: Initially the adult female stood alone on a section of vertical bark. She made a directed walk into a group of ten closely associated offspring and gently stroked them with her whips. The young moved to surround and orient to her, and stroked her in return, touching her whip, pedipalps, and legs. Of these ten young, the mother made individual contact with seven of them over ~4 minutes. Although the young initially had been sitting close together, slowly waving their whips, once the adult female joined the group the youngsters' whip movements quickened so that most of the young contacted one another as well as the female. Then the mother walked directly to a separate group of two youngsters five body lengths away, engaged in mutual stroking for ~30 seconds. Next she walked

directly to a third group of five young on the opposite side of the cage and repeated the interaction for several minutes, before returning to sit in the middle of the first group. In each case, the young oriented towards the mother and were tactilely interactive. The interactions were deliberately initiated and appeared to be affiliative behavior between the mother and her offspring.

Immature *D. diadema* (Groups 4–8) remained closely associated and interactive with their siblings until they reached sexual maturity between 13 to 15 months old (Fig. 5–9). For the first few weeks to a month after descending from the mother's dorsum the young clustered tightly around their mother (see Figs. 17, 18). The young surrounded their mother, sat beneath her, or hid in small cracks on the cork bark nearby. As they matured, the young distributed themselves more widely through the space available in the cage but continued to aggregate in sibling groups or in groups near the mother, with only a few individuals found solitarily until reaching sexual maturity (Figs. 8, 9).

The mother's physiological state affected the duration and amicability of the mother-offspring association. Based on our observations, for several weeks prior to molting some of the mature females actively moved away from her offspring, reduced interaction rates, and in Group 4 became agonistic. In the wild, premolt behavior could be a time when the female permanently leaves the young. In captivity, the females reinitiated "amicable" (tolerant, nonaggressive) interactions with offspring and returned to rest in the middle of young soon after molting.

Constant whip contact among immature amblypygids characterized aggregations. For immature *D. diadema*, the average nearest neighbor distance was significantly less than the extended length of the whips, indicating that individuals positioned themselves close enough for tactile interactions with their neighbors (Figs. 10, 11). Nearest neighbor distances among individuals in groups were consistently small relative to the size of the animals. Although nearest neighbor distances increase with the increasing size of the animals, the tendency to aggregate and the size of groups remained fairly constant (Figs. 10, 11).
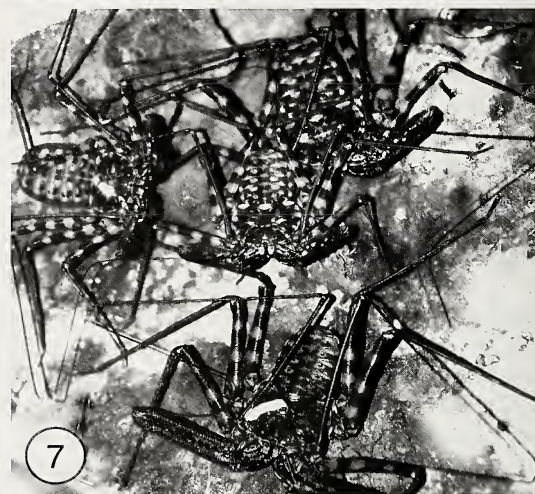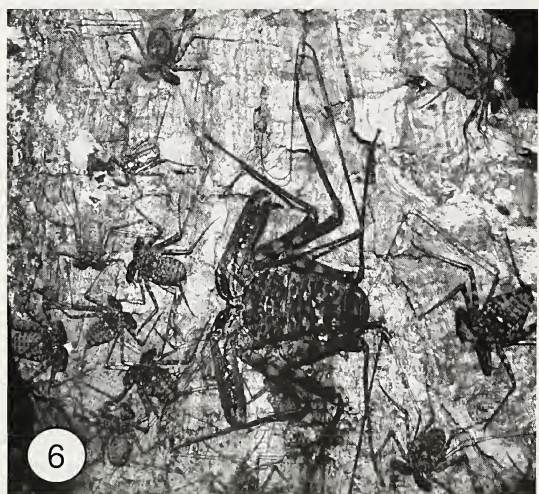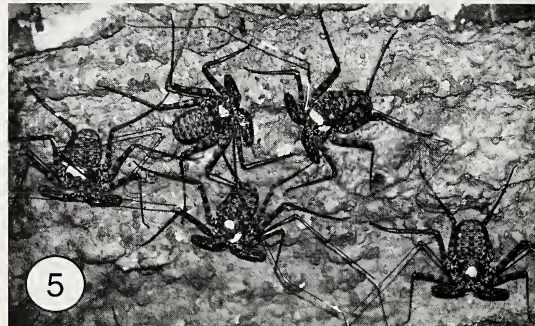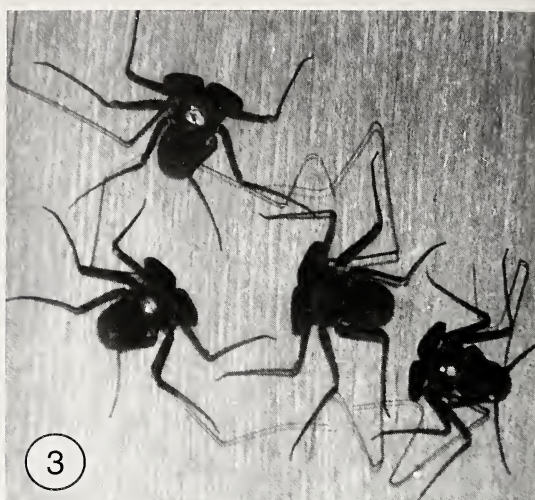
Figures 2–7.—Photographs of typical amblypygid associations at different ages. Note the extent of whip contact among individuals and the closed, non-aggressive positions of the palps. 2. Three *Phrynus marginemaculatus* young (Group 2) oriented to and interacting with their mother at age 2 months. Two additional individuals are under the adult female's left legs. 3. *P. marginemaculatus* adults (Group 3) on uniform plywood bark. 4. Amicable interactions among 9-month old *P. marginemaculatus* from Groups 1 and 2 (distinguished by the presence or absence of a white dot on the carapace) that had been combined 2 days previously. 5. *Damon diadema* young (Group 5) at age 6 months. 6. Adult female *D. diadema* and 13 of her 10-month old offspring (Group 6). Note that the group was not limited to the small space shown, but had 4,446 cm² of suitable bark throughout the cage. 7. *Damon diadema* offspring at age 13 months (Group 4). The male on the left (wider, thinner palps) molted to sexual maturity before his three sisters.
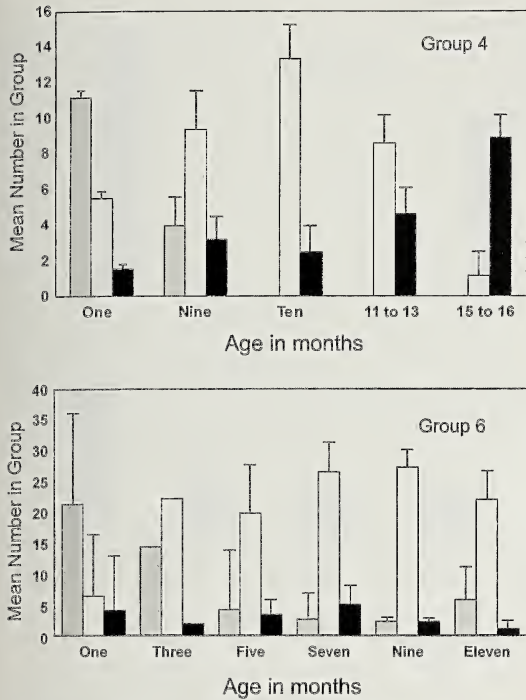
Figures 8-9.—Mean number (+SD) of *Damon diadema* young found in association with their mother (grey bars), siblings only (white), or found solitarily (black) at different ages. Group 4 was composed of 18 siblings and their mother until they were 10 months old, when two subadults died of natural causes. The adult female was removed when the offspring were 11 months old, due to her increasingly aggressive interactions with her offspring. Between age 13 and 15 months, the amblypygids reached sexual maturity. By the time the siblings were 15 months old, 7 siblings died after losing appendages during aggressive interactions or starved while evading their more aggressive siblings, resulting in n = 10 adults. Mean numbers per group were based on 8–15 observations per month. Group 6 was composed of 38 siblings and their mother. All siblings were present until age 11 months when eight subadults died. The mother remained with her offspring throughout these observations. Mean number of animals in each category per month was based on 3 or more observations (range n = 3–10 observations/month), except for when the animals were 3 months old (observation n = 1).

In both *D. diadema* and *P. marginemaculatus* we observed frequent whip contact and few aggressive interactions among immature siblings until sexual maturity. Familiar individuals were almost always approached directly, rather than avoided, and were greeted with repeated stroking of the whips. In both species, agonistic interactions were mild and infrequent *prior to* sexual maturity. Aggression was rarely observed among immature siblings and their mothers, and among familiar adult *P. marginemaculatus*. Often when an animal entered a tight aggregation of other individuals, others briefly opened their palps in a mild threat display. However, within a few seconds, they would close their palps and stroke the individual with their whips. The animal would rapidly settle into the group without any further evidence of aggression. We found no evidence of cannibalism or missing appendages attributable to aggressive interactions in immatures.

Sexual maturity in *D. diadema*, starting at age 12–13 months, was characterized by distinct morphological and behavioral changes. Within a clutch, molting to maturity varied by as much as two months. Although they were slightly smaller than older adults when they molted to sexual maturity, it is at this molt that males acquire the characteristically elongate, thin palps of adult males. In contrast, adult female palps remain short and wide at sexual maturity. Upon sexual maturity, aggregation patterns changed dramatically as individuals spread out widely and were more likely to be solitary (Fig. 8–11). Although we rarely observed siblings fighting during the day, only at the onset of sexual maturity were animals found with injured legs or whips. Smaller individuals starved as they attempted to avoid aggressive males by remaining on the "ceiling." Males persistently courted their sisters and threatened their brothers. Members of some groups were separated soon after maturity to minimize mortality.

Adult Dynamics.—Unrelated adults of *D. diadema* (Group 9) were solitary and widely distributed in the cage, except when male-female pairs were courting (Fig. 12). Non-courting individuals stayed far apart from one another, with an average nearest neighbor distance of 22.0 cm. In contrast, courting male-female pairs were on average only 6.75 cm apart, closer than the average adult whip length of 11.56 cm. Courting pairs were within ready whip contact with each other, while non-courting adults positioned themselves far enough apart that they were not in contact with one another except during infrequent interactions.
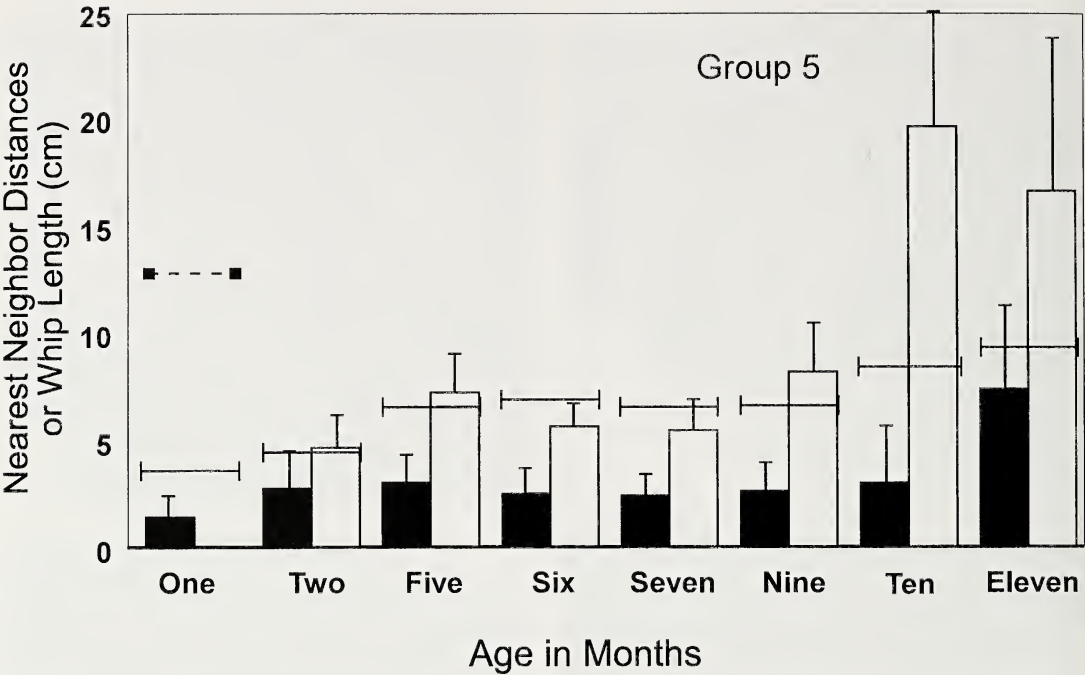
Figure 10.—Nearest neighbor distances among *Damon diadema* in Group 5 relative to whip length for individuals in sibling groups (black bars) and solitary individuals (white) at different ages. Mean whip length of the young (l——l) and their mother (l– – –l) is indicated. Individuals in groups of siblings sit significantly closer together than necessary to make whip contact with one another.
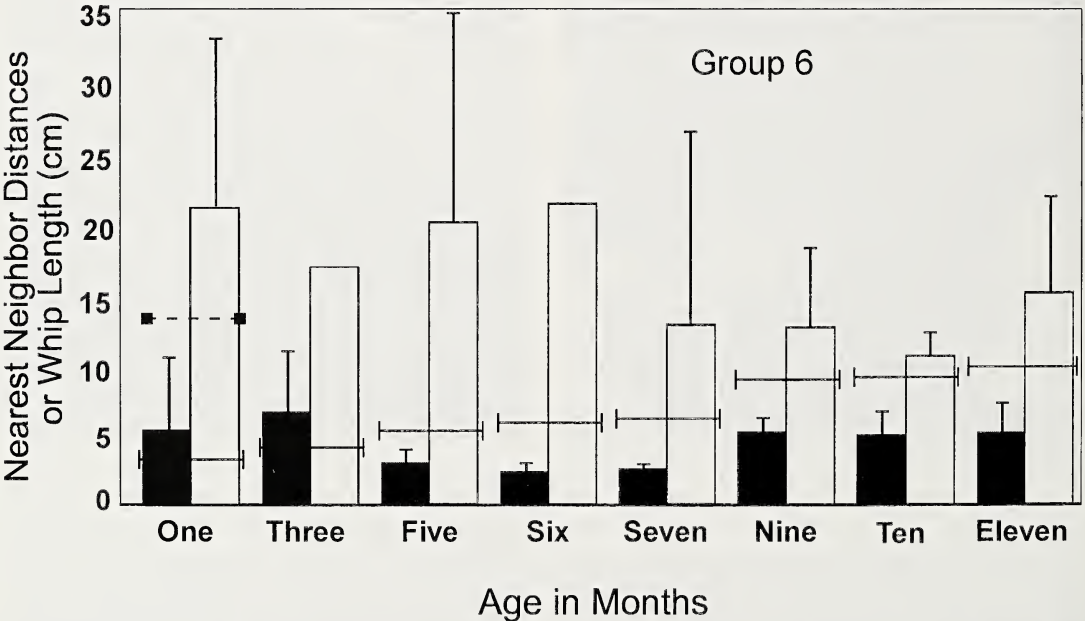

Figure 11.—Nearest neighbor distances among *Damon diadema* in Group 6 relative to whip length for solitary individuals and individuals in sibling groups at different ages. See Fig. 10 for explanation of symbols.
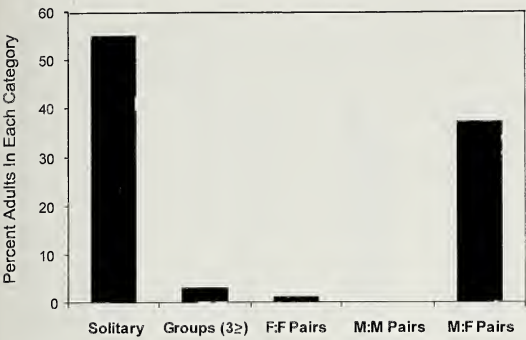
Figure 12.—Percent of the nine adult *Damon diadema* (Group 9) found solitarily or with other individuals during observations (*n* = 27) from September 2000 to February 2001.

When same sexed adults of either species were newly introduced into the same cage when establishing the colonies or due to temporary removals, fights invariably occurred similar to those described by Alexander (1962), Weygoldt & Hoffmann (1995), and Weygoldt (2000). Fighting among adult *D. diadema* was rarely observed, but adults were twice cannibalized and injuries occurred oc-

casionally. Conflicts among adult *P. marginemaculatus* were short-lived and rarely led to injury.

Evidence of Aggregation in Immatures.—Ten-month old *D. diadema* (Group 4) did not distribute themselves evenly or randomly on the available bark surface (Fig. 13). Rather, individuals aggregated in higher densities than expected in some areas, while others had lower densities than expected from a random distribution. The mean observed spatial distribution within the cage, based on observations over 19 days, differed significantly from the expected random distribution (Fig. 13, $\chi^2 = 23.5$, $df = 5$, $P < 0.01$). Moreover, analysis of individual daily distributions demonstrate that aggregations did not just occur in certain 'prime' locations that attracted many individuals, but that the site of aggregations varied daily indicating preferences for being in a group rather than for specific favorable locations.

Costs and Benefits of Aggregation.—*Manipulation of Spatial and Textural Uniformity:* Spatial and textural features of the cage mi-
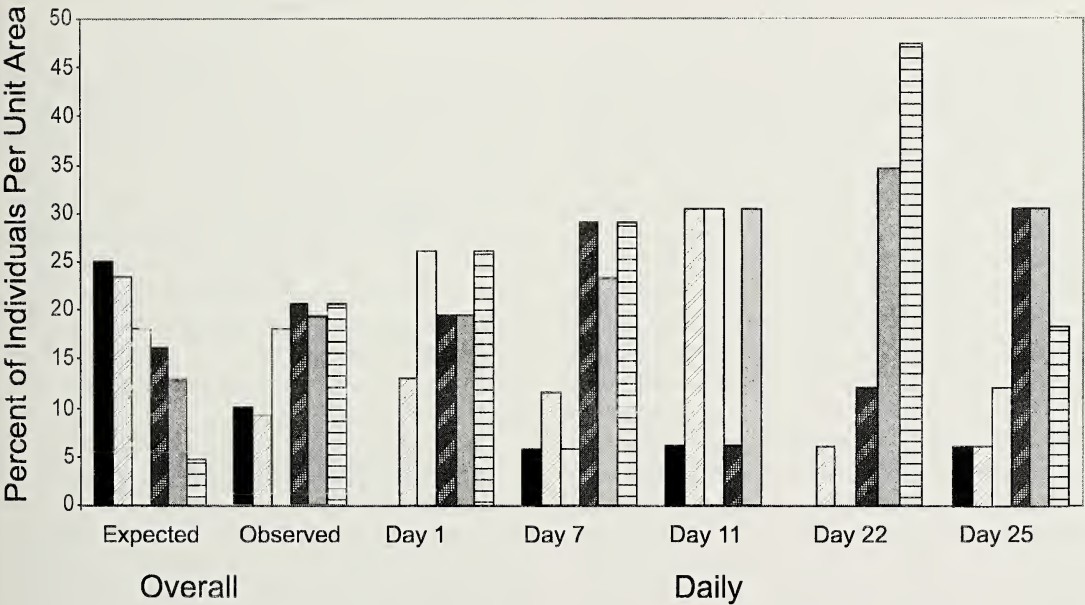
Distribution of Individuals on Bark

Figure 13.—Overall expected, observed, and five daily spatial distributions of *Damon diadema* (Group 4) on different sized pieces of cork bark in their cage. Expected values are based on the expected number of individuals per piece of bark unit area assuming a random distribution. Each bar represents the observed percentage of individuals on each piece of bark, with each bar pattern and location in the figure unique to a given piece of bark.
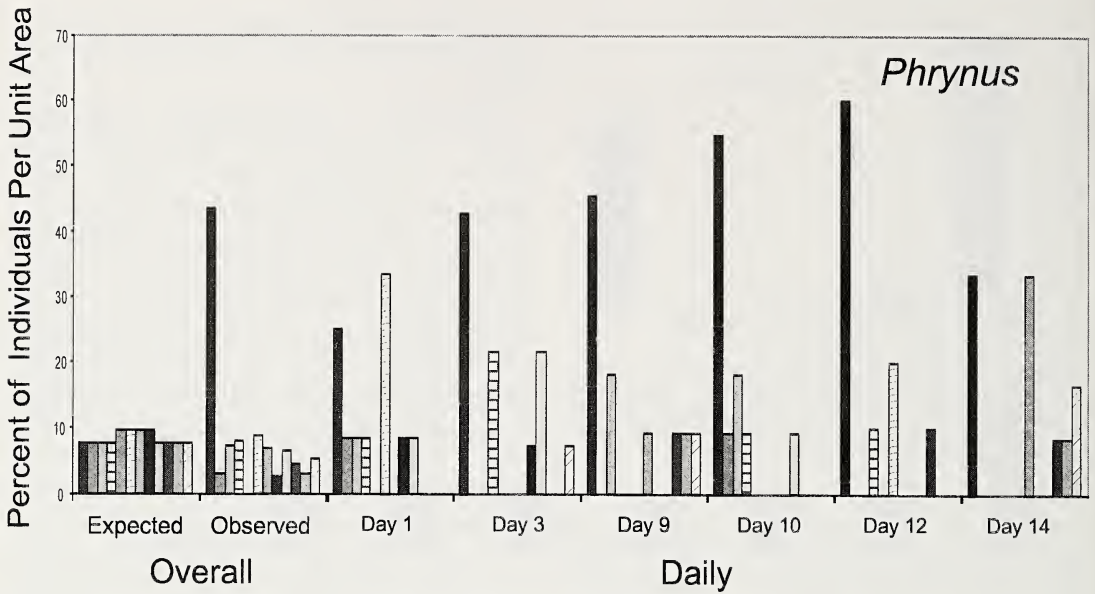
Distribution of Individuals on 'Uniform' Substrate

Figure 14.—Overall expected, observed, and daily spatial distributions of adult *Phrynus marginemaculatus* (Group 3) on texturally and spatially uniform plywood "bark". The amblypygids distributed themselves non-randomly relative to the space available on the bark, with more individuals in groups than expected on a daily basis. Each bar represents the observed percentage of individuals on each piece of bark, with each bar pattern and location in the figure unique to a given piece of bark.

croclimate did not appear to be the only factor driving the formation of aggregations, since aggregations still occurred on uniform plywood surfaces. *P. marginemaculatus* (Group 3) and *D. diadema* (Group 4 at age 14 months) still formed aggregations when housed in cages with a uniform plywood habitat. The mean distribution of *P. marginemaculatus* over the entire experimental period differed significantly from the expected random distribution (Fig. 14, $\chi^2 = 22.3$, $df = 11$, $P < 0.05$). However, this was a result of a single "hot spot" in the cage where one aggregation consistently occurred. In other areas of the cage, distributions changed on a daily basis and on five of the six days observed, the distribution differed significantly from the expected random distribution. In contrast, the mean distribution for the immature *D. diadema* taken over the entire experimental period did not differ significantly from the expected random distribution (Fig. 15, $\chi^2 = 7.67$, $df = 5$, $P > 0.05$)), indicating that over the experimental period the animals used different locations of the wood surface equally. However,

closer examination of daily distributions demonstrates that individuals were found in groups, but that the location of these aggregations was in constant flux.

Manipulation of Food Abundance: Manipulation of food abundance did not significantly affect the tendency of individual *P. marginemaculatus* to disperse or aggregate. There was not a significant difference in nearest neighbor distances between individuals in food-deprived and food-surplus situations ($t = 1.28$, $df = 15$, $P > 0.05$).

Unlike many social spiders (Whitehouse & Lubin 2005), no amblypygids were observed to engage in cooperative capture of large prey items throughout the entire study. Prey sharing was observed on rare occasions in both species (< 7 occasions for each species) in hundreds of hours of observation. Once, two 7-month old *D. diadema* shared prey for a ten-minute period before pulling it apart. In a *P. marginemaculatus* mother-offspring group kept by a student of LSR, three 12-month olds shared pieces from a large cricket that was being consumed by their mother (C. Fishel,
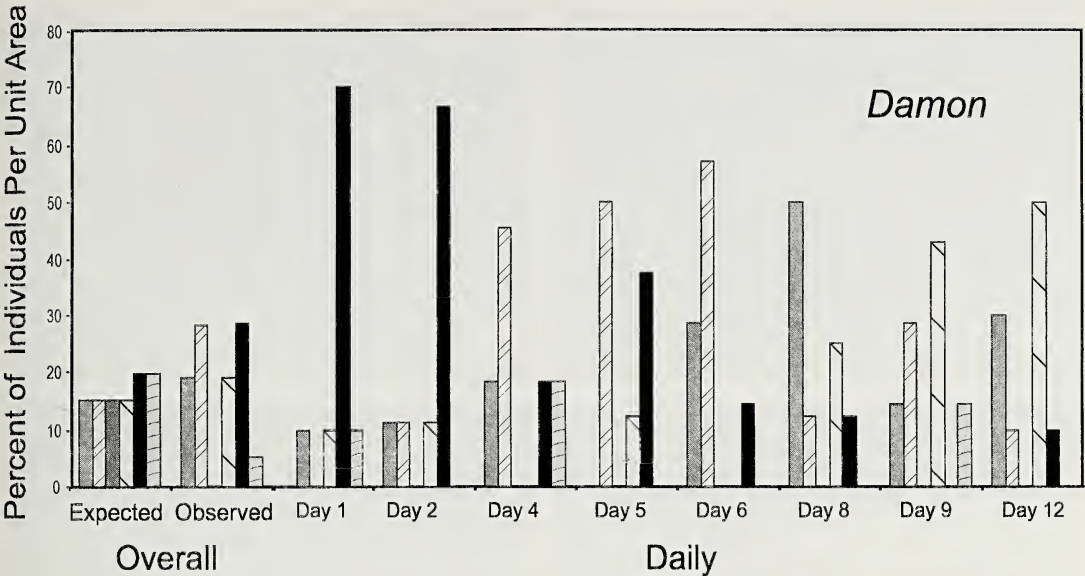
Distribution of Individuals on 'Uniform' Substrate

Figure 15.—Overall expected, observed, and daily spatial distributions of subadult, 14-month old *Damon diadema* (Group 4) on texturally and spatially uniform plywood "bark". Each bar represents the observed percentage of individuals on each piece of bark, with each bar pattern and location in the figure unique to a given piece of bark.
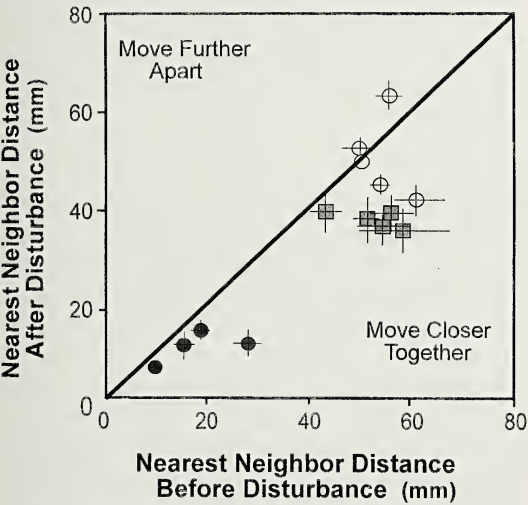
Figure 16.—In response to disturbance, *Damon diadema* (Groups 5 and 8) aggregated together significantly more than expected. Data show the ratio between the mean nearest neighbor distances immediately before and four minutes after a disturbance. Circles represent replicates of Group 5 at age 1.5 months (< 30 mm) and at 8 months (> 40 mm). Squares represent Group 8 at age 2months. Mean Standard Deviation for nearest neighbor distances before (vertical lines) and after (horizontal lines) are indicated in each datum.

pers. comm.). Although prey-stealing was uncommon when the animals were well-fed, immature *D. diadema* were observed stealing food from one another after being food deprived for only three days. On three occasions, individuals were observed successfully stealing a cricket from another individual. In each of these cases, the individual who stole the food returned to a tight aggregation of its siblings and, consequently, the food was stolen again by a third individual. Short feints toward siblings with prey occurred in both species occasionally, but longer chases were not observed.

Response to Disturbance and to a Potential Predator: Solitary amblypygids rapidly run away from threats in the field or in captivity (pers. obs.). Group dynamics when disturbed are striking. In response to their cages being rattled for fifteen seconds, young *D. diadema* significantly reduced their nearest neighbor distance to siblings (Fig. 16; Treatment effects $F_{1,22} = 15.81$, $P < 0.0006$). In response to the disturbance, many young amblypygids scuttled under their mother (Figs. 17, 18). Reductions in nearest neighbor distances among replicated disturbances within groups were not
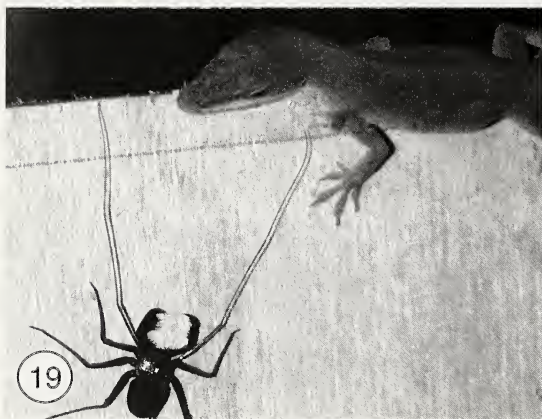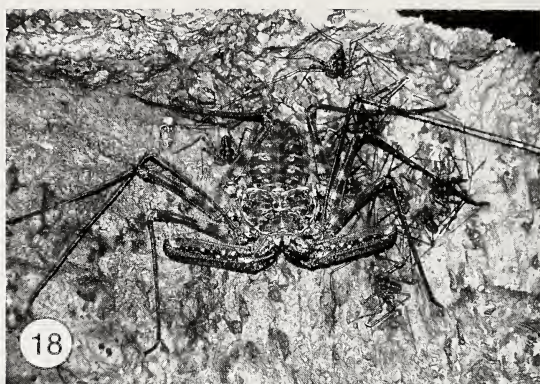
Figures 17—20.—Responses of amblypygids to external factors. 17. *Damon diadema* (Group 5) at age 1.5 months prior to disturbance. 18. *D. diadema* (Group 5) immediately after disturbance. Note that some young moved beneath their mother. 19, 20. Investigation of lizard (*Anolis carolinensis*) by a subadult *Phrynus marginemaculatus* and an adult *D. diadema*, respectively.

significantly different from zero. There was a highly significant group (= age) effect detected as well, as the younger groups were more likely to move closer together than were older animals (Fig. 16, $F_{2,22} = 87.0$, $P < 0.0001$, $t = -12.31$, Tukey-Kramer adjustment $P < 0.0001$, $df = 22$). Mean group size increased in Group 5 at 2 months in response to disturbance (Paired t-test, $t = -4.34$: Before, x $\pm$ SD = 24.6 $\pm$ 6.8; After, 34.6 $\pm$ 2.5; $P < 0.012$). But group size did not significantly change with disturbance for Group 6 at either 1.5 months ($t = -2.03$: Before, 18.2 $\pm$ 6.2; After, 20.5 $\pm$ 6.1) or at 8 months ($t = -0.77$: Before, 32.7 $\pm$ 3.8; After, 34.7 $\pm$ 3.9). On several occasions during transfers between cages, an adult female with 7-month old offspring attempted to defend her young by an (effective) threat display and attack on the researchers (Walsh & Rayor pers. obs.). The female raised her body high above the substrate,

opened her palps widely (~130° angle), and slowly stalked toward the offending hand(s). When we did not move back, she rapidly closed the palps and attempted to stab us with the stiletto-sharp terminal claw of her distitarsus.

Our attempts to elicit antipredatory behavior through the introduction of an insectivorous lizard were unsuccessful, as none of the amblypygids (of either species) were apparently threatened by the presence of the lizard. In contrast, the lizard evoked active exploration on the part of the amblypygids (Figs. 19, 20). Most individuals readily approached the lizard and repeatedly touched the entire length of the lizard's body and tail with their whips. In most cases, individuals extended their palps in what appeared to be a threatening behavior (similar to the behavior seen between two fighting individuals or similar to the hunting position prior to attack). Even a small year-

old *P. marginemaculatus*, with a body length of 6 mm, walked directly up to the lizard and touched its whips along the entire length of the lizard's body for five minutes, and then walked away (Fig. 19). We were unable to determine if the amblypygids responded to the lizard as a potential, albeit very large, prey item or were simply curious about the novel creature in their cage.

DISCUSSION

Mother-Offspring-Sibling Interactions.— Our results demonstrate that, at least in captivity, young *P. marginemaculatus* and *D. diadema* remain closely associated and highly interactive with their mother and siblings for approximately one year. Interactions include both active aggregation and frequent amicable tactile interactions regardless of substrate features. Individuals aggregated on a variety of surface textures and locations that varied daily, rather than aggregating only on preferred microhabitats.

The social interactions observed among conspecifics of the two species were not identical. *P. marginemaculatus* were tolerant and interactive, and they readily formed multigenerational aggregations into adulthood. In contrast, *D. diadema* siblings were highly tolerant and interactive only until they reached sexual maturity at ~13 months old. After sexual maturity behavioral interactions were more agonistic, and individuals moved apart. Adults were essentially solitary, except during courtship, closely aligning with the description of adult amblypygids in the literature.

Should our observations on social behavior in amblypygids be considered an artifact of captivity? We do not think so. Although behavioral observations of immature amblypygids in the field are clearly necessary, these species are unlikely to be primarily solitary with only transient maternal care (see Table 1). The vast majority of solitary predaceous arachnids are cannibalistic, and keeping kin together to force sociality typically results in a group size of one. The behaviors of asocial animals that survive group situations are dominated by agonistic and territorial interactions. On the contrary, the two species of amblypygids displayed social tolerance, long-term associations, extensive tactile interactions, and an absence of cannibalism that more closely resemble the social dynamics of the better

known subsocial and social species of spiders and other arachnids (Tables 2, 3). However, there is some evidence that these traits may be facultative, e.g., subsocial scorpions and spiders, where abundant food and limited dispersal options in captivity may delay dispersal and reduce conflict compared to the same species in the field (Gundermann et al 1993; Schneider 1995; Kim 2000; Mahsberg 2001; Mahsberg pers. comm.). Similar factors may have influenced the duration of tolerance and association among the amblypygids in this study but are unlikely to have structured the overall social pattern of interactions. Field studies that focus on the ontogeny of behavioral dynamics in immature amblypygids will clarify the duration of association and patterns of sociality in *P. marginemaculatus* and *D. diadema*.

As the amblypygids in this study are in distantly related families from different continents but still share aspects of their social interactions, similar patterns among mother-offspring-sibling groups of immature amblypygids may be predicted in other species. Other species of amblypygids that have been reported to be highly tolerant warrant further investigation, particularly *Heterophrynus longicornis* in Amazonia (Weygoldt 1977), and *Phrynus asperitipes* (Quintero 1981) and *Acanthophrynus coronatus* Butler 1873 both of Mesoamerica.

Costs and Benefits of Aggregation.— Benefits of living in social groups often include increased prey capture or a reduction in predation risk (Alexander 1974; Rayor & Uetz 1990, 1993). Whitehouse and Lubin (2005) suggest that benefits of sociality in the spiders can be broken down into either foraging or defensive advantages, but not reproductive advantages. The amblypygids did not hunt cooperatively or share prey, although they may benefit by advanced notice of the presence of prey by their neighbors' heightened whip activity. As food abundance increases tolerance in solitary spider species (see Uetz & Heiber 1997), we predicted that food-deprived individuals would be less tolerant and more spread out to reduce competition. On the contrary, manipulation of food availability did not alter aggregation levels of *P. marginemaculatus*, suggesting that the tendency to aggregate was not directly related to prey capture or hunger level. Because many arachnids can sustain long periods of time without food, it

is possible that, had the food deprivation level been more extreme, we would have seen more dispersion or greater competition over prey. Regardless, foraging benefits are unlikely to be the primary explanation for social aggregation in these species.

Active defense of young and even cooperative defense is found in a number of the social arachnids (Buskirk 1981; Polis & Lourenco 1986; Mori & Saito 2005; Table 1). When frightened, young *D. diadema* moved significantly closer to their mother or siblings (Fig. 18), and mothers threatened or actively attacked human "aggressors." Antipredator strategies in all amblypygids include nearly constant movement of the sensory whips providing acute awareness of their surroundings, rapid movements away from the threat, and dorso-ventrally flattened bodies which fit into extremely thin crevices (Weygoldt 2000). Field observations of predation are extremely rare: only Hebets (2002) reports observations of a single *Phrynus parvulus* Pocock 1902, being consumed by a scorpion and Adrian Barnett (pers. comm.) has observed a *Heterophrynus batesii* Butler 1873, captured by a neotropical primate, the golden-backed uacari (*Cacajao melanocephalus ouakary*). Whether a benefit of social grouping in amblypygids includes a reduction in predation risk will require manipulative field experiments, but advantages related to group defense are probable, especially in younger animals.

Our attempts to assess the social consequences of predation risk from a putative predatory lizard resulted in distinctive investigative behavior rather than evasive behavior in amblypygids of both species. A general tendency to investigate all aspects of their surroundings could help explain their continuous whip exploration of neighboring individuals.

In summary, our observations suggest that at least two species of amblypygids display social behaviors significantly more complex and prolonged than those characteristic of early maternal care.

A Reassessment of Social Patterns in Arachnids.—Parental care is defined as parents directly or indirectly investing in their offspring's fitness (Clutton-Brock 1991). "Subsocial" behavior in invertebrates is a subset of parental care provided to offspring that have emerged from the egg sac and which increases the survival of the offspring (Wilson

1971; Tallamy & Wood 1986). However "subsocial" has been used as a collective term to lump all associations from transient parent-offspring associations ("early parental care," Table 1) to much more complex social groups that include long-lasting mother-offspring-sibling associations extending until or even beyond sexual maturity of the offspring and the death of the mother (Table 2). "Sociality" has typically been defined as involving some level of cooperation, communication, and prolonged tolerance in groups of conspecifics (Kullmann 1972; Buskirk 1981; Costa & Fitzgerald 1996; Krause & Ruxton 2002). Unfortunately, there is often no clear division based on the complexity of the social behavioral repertoire, duration of associations, and social demographics, between the more advanced "subsocial" species and "social" arachnids. The use of "subsocial" terminology masks the social diversity among the arachnids that provides insights into the evolution of group-living. Over the last decade, there has been an increasing recognition that sociality occurs along a behavioral continuum, rather than in discrete categories, and that definitions of sociality need to be broadened to more accurately reflect the diversity of social dynamics in a broad range of animals (e.g., Sherman et al. 1995; Costa & Fitzgerald 1996; Choe & Crespi 1997; Crespi & Choe 1997; Whitehouse & Lubin 2005; Costa & Fitzgerald 2005). Wcislo (1997) suggests that in describing arthropod social organizations it has been too easy to use a terminology that *categorizes* the group, but does not actually describe the behaviors or traits that occur in these groups, such that natural variation within or between social species is missed. As Wilson (1971, p. 5) states "[A society] is a group of individuals that belong to the same species and are organized in a cooperative manner. I believe the terms society and social must be defined quite broadly in order to prevent the arbitrary exclusion of many interesting phenomena. . . . Not only eusocial insect colonies but also most parasocial and subsocial groups should be designated as societies and their members as social in the most general sense."

Here we propose that in describing and assessing social dynamics in "subsocial" arachnids, it is past time to take into account both the duration and patterns of association among

mothers, offspring, and siblings. Key variables are the age of dispersal from the natal group, social demography, extent of cooperative behavior, and patterns of tolerance or amicable interactions within the social group. It is through incremental changes in these variables along the social continuum that higher sociality evolves. Because the term "subsocial" is so firmly entrenched in the literature as an evolutionary pathway from which cooperative spiders and eusocial insects have evolved, we feel it is impractical to suggest that it be eliminated. Instead, we propose that in future studies the terminology be modified to "transient subsocial" to describe transient parental care of eggs and young instars, such as seen in many arachnids and other arthropods (*sensu* Tallamy & Wood 1986). We propose that "prolonged subsocial" be used to describe species with complex and long-term associations between mothers and offspring or sibling groups that may extend up to or beyond sexual maturity, in which the associations do not last until there are multiple breeding adults within the group. We encourage the recognition that "prolonged subsocial" associations are, indeed, social groups in the broader use of the term (*sensu* Wilson 1971; Costa & Fitzgerald 1996, 2005). By this definition, both *D. diadema* and *P. marginemaculatus* live in prolonged subsocial groups.

We recognize that duration of association is a continuum and may vary with ecological factors, but general patterns of association are found in different taxa. Most arachnid orders have species that we characterize as "transient subsocial." They exhibit early parental care with maternal (and in opilionids paternal) defense of eggs, as well as a brief association of newly emerged young (first and rarely second instar) with their mother prior to independent foraging and explosive dispersal from the natal nest (Table 1: Uropygi (Thelyphonida), Amblypygi, Schizomida, some Araneae, Pseudoscorpiones, Scorpiones, Acari, Solfugae, Opiliones). However, more prolonged associations between mothers and offspring, and siblings are rare among the arachnids and are only described in a few species per order (Table 2: Araneae, Amblypygi, Scorpiones, Pseudoscorpiones, Acari).

Of the approximately 39,000+ identified spider species less than 0.2% (55 colonial and cooperative species, 18 *Argyrodes* sp.) are social (Whitehouse & Lubin 2005; Platnick 2006). Perhaps another 0.06% (21 species) of spiders show social tendencies greater than transient early parental care (Whitehouse & Lubin 2005; Tables 2, 3). Among the approximately 45,200 Acari, there are ~13 (0.0001%) social species, primarily spider mites in the Family Tetranychidae (Saito 1997; Mori & Saito 2005). Of the ~10,525 species in the other arachnid orders (Coddington & Colwell 2002; Harvey 2003), there are approximately 0.15% (16 species) that show evidence of social traits beyond early parental care (Tables 2, 3). Some of the smaller arachnid groups, such as the 78 species of Palpigradi and 55 Ricinulei species, are so poorly known that no conclusions can be made about their social tendencies. Of the 23 social arachnid species (excluding the six non-tetranychid acarines for which little demographic data is available, Saito 1997, pers. comm.), 14 live in prolonged subsocial groups (amblypygids, scorpions, spider mites), while 9 are unquestionably "social" characterized by long-lasting groups with multiple breeding adults (pseudoscorpions, scorpions, spider mites). Thus, well over 99% of all arachnids are solitary, while perhaps as many as 0.05% exhibit social tendencies allowing largely predaceous creatures to live in groups for some extended period in their lives. As predators, the longer the parent(s) and siblings remain together, the greater the immatures' predatory capabilities and need for prey, and the more precarious the balance between the benefits of cooperation and costs of conflict inherent in all social groups (Krause & Ruxton 2002). Elucidating the selective factors that have enabled this tiny percentage of the arachnids to live in social groups is important to understanding the evolution of the arachnids, and the evolution of sociality generally.

Within the arachnids, there is a continuum between the prolonged subsocial and social species. The only obvious feature that separates these two groups is the presence or absence of multiple breeding females within the social group. The continuum ranges from relatively brief associations of mothers with their young offspring or within sibling groups (e.g., Schneider 1995; Kim 2000), associations that last for long developmental periods prior to sexual maturity (e.g., Polis & Lourenco 1986; Evans 1998; Mahsberg 2001; this study), long

lasting groups with multiple breeding females (Brach 1978; Polis & Lourenco 1986; Zeh & Zeh 1990; Saito 1997; Mori & Saito 2005), and the complex sociality of the cooperative spiders (Aviles 1997; Whitehouse & Lubin 2005).

Patterns of social behavior among the spiders have been well documented (Buskirk 1981; Aviles 1997; Uetz & Heiber 1997; White-house & Lubin 2005) and will not be repeated here except in comparison to the other social arachnids. Traits that are characteristic of colonial and cooperative social spiders include: (1) Prolonged association with conspecifics, (2) a high level of tolerance, (3) a strong tendency to aggregate, (4) overlapping generations of kin, (5) communicative behavior, (6), cooperation in prey capture, retreat construction, or defense, (7) a lack of colony identity (but see Rowell & Aviles 1996 for an exception), and (8) the presence of silk webs that facilitate cooperative prey capture and intra-specific communication (Kullmann 1972; Buskirk 1981; Aviles 1997). Many of these behavioral traits are present in the other social arachnid species (Table 3), but not in those species with only transient parental care ("transient subsociality"). The first three traits and communicative behavior are typical for the prolonged subsocial and social species. Prolonged subsocial species do not have overlapping generations of adults by definition, but offspring may overlap with their mother up until sexual maturity. The extent of cooperation varies among the groups, although the amblypgyids are notable in not overtly cooperating on anything. The lack of colony identity has not been examined in most of the social arachnids, although *D. diadema* demonstrates differential behavior toward kin and non-kin (Walsh & Rayor, unpub. data). Among the non-spider arachnids, shared silken retreats can only be produced by social spider mites and pseudoscorpions (Brach 1978; Mori & Saito 2005; Tizo-Pedroso & Del-Claro 2005). In both groups, the silk is used to construct retreats rather than prey capture webs.

We argue that sociality should not be characterized *strictly* based on traits that are typical of members of a few spider families at the high end of the social continuum. Rather, such definitions should reflect common variables such as the age of dispersal from the natal group, social demography, extent of cooperative behavior, and patterns of tolerance or amicable interactions within the social group. Studying the diversity and complexity of social behaviors in arachnids without applying the expectation that they will replicate *all* of the characteristics of the cooperative spiders (or eusocial insects, for that matter) will help elucidate general patterns in social evolution.

One form of "social" grouping in arachnids that we could not readily classify using this scheme were the temporary aggregations of (apparently) unrelated subadult and adult opilionids, pseudoscorpions, and scorpions (Weygoldt 1969; Polis & Lourenco 1986; Coddington et al. 1990; Machado & Vasconcelos 1998; Machado 2002) (Table 3). These aggregations are characterized by tolerance, preference for close contact with others, and cooperative defense from predators. Most occur in potentially limited habitats and may be associated with increased humidity or, in pseudoscorpions, opportunities for phoresy, but do not seem to be truly social groups by most definitions.

In summary, social behavior is rare among the arachnids. Rare behaviors provide the opportunity to pose ecological and evolutionary questions about the costs and benefits of group living. Here we have described two amblypygid species that clearly display some social behaviors characteristic of the other social arachnids, but are also not identical in all features. Further, we suggest that a broader terminology and clearer descriptions of the duration of association and the patterns of social behaviors will aide in our understanding of group-living among arachnids and the evolution of sociality.

ACKNOWLEDGMENTS

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THE PREY OF THE LYNX SPIDER *OXYOPES GLOBIFER* (ARANEAE, OXYOPIDAE) ASSOCIATED WITH A SEMIDESERT DWARF SHRUB IN AZERBAIJAN

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ABSTRACT.   The prey of the lynx spider, *Oxyopes globifer* Simon 1876, occurring on *Salsola nodulosa* (Moq.) plants, was analyzed. In common with other cursorial spiders, the percentage of feeding specimens in the population of *O. globifer* was low (5.5%). Males were observed feeding significantly less frequently than females and immatures of both sexes. After oviposition, however, the records of prey capture in egg-guarding females also declined considerably. *Oxyopes globifer* is a polyphagous predator feeding on a wide range of arthropods: insects of the orders Hymenoptera, Diptera, Lepidoptera and Homoptera, as well as on several spider species. The primary food was worker ants, which accounted for 62.7% of total prey. No other prey taxon was present in any considerable percentage. *O. globifer* captured prey ranging between 22.7 and 243.8% (mean 88.8%) of its own body length. Most frequently taken were medium-sized arthropods varying from 50–110% of spiders' body lengths.

Keywords: diet, myrmecophagy, prey length, semidesert, Azerbaijan

Most lynx spiders (Oxyopidae Thorell 1870) are typical cursorial hunters, which possess relatively keen eyesight and do not use silk for prey capture (Kovoor & Munoz-Cuevas 1997). Instead, they actively pursue their prey and seize it with a short lunge (*Oxyopes* Latreille 1804) or attack it from ambush (*Peucetia* Thorell 1869) (Rovner 1980).

In common with other cursorial spider groups, the literature on prey of Oxyopidae is scarce. Exceptions are the striped lynx spider, *Oxyopes salticus* Hentz 1845 (Lockley & Young 1987; Nyffeler et al. 1987b, 1992; Agnew & Smith 1989; Bardwell & Averill 1997), and the green lynx spider, *Peucetia viridans* (Hentz 1832) (Turner 1979; Randall 1982; Nyffeler et al. 1987a, 1992; Quicke 1988), both being from North America. Less extensive quantitative data are available on the natural prey of *Oxyopes apollo* Brady 1964 from the USA (Agnew & Smith 1989), and *O. licenti* Schenkel 1953 and *O. sertatus* L. Koch 1877 from Japan (Furuta 1977).

The present paper is the first study of the prey of the Mediterranean lynx spider, *Oxyopes globifer* Simon 1876, which occurs in North Africa, Southern Europe, Near East and Central Asia (Levy 1999). In Azerbaijan, individuals of this species are frequently found on dwarf shrubs *Salsola nodulosa* (Moq.), *Artemisia fragrans* (Boiss.), and *Noaea mucronata* (Forssk.). *O. globifer* has an annual life cycle. Adult specimens appear at the end of May and

mating lasts throughout June. At the beginning of July males disappear, while females start to produce egg sacs, which they attach to the branches of shrubs. Females attend their cocoons until the young emerge. Breeding season runs until mid September and individual females usually produce several egg sacs during this period (Huseynov unpubl. data).

The investigation was carried out on the Apsheron Peninsula in Azerbaijan. The study site was located near Yeni-Surakhany village (40°42′N, 49°95′E). This was an open area of ephemeral semidesert covered with dwarf shrubs *Salsola nodulosa*, *Alhagi pseudoalhagi* (M.B.) and short grasses, predominantly *Calendula persica* C.A.M., *Senecio vernalis* Willd. & Kar., *Medicago denticulata* Willd., *Carduus arabicus* Jacq., *Erodium cicutarium* (L.), *Pterotheca marschalliana* (Rchb.), *Poa bulbosa* L., *Anisanthea rubens* (L.) and *Aegilops biuncialis* Vis.

O. globifer was abundant only on *Salsola* shrubs, therefore observations were concentrated exclusively on this plant. Sixteen surveys were conducted from 20 May–9 September 1998 and took 27.5 h in total. All observations were made in daylight between 12:00 and 18:00 h. During surveys, *Salsola* shrubs were thoroughly searched for spiders, and each individual *O. globifer* found was captured in a transparent glass vial. In the vial the spider's mouthparts were inspected with a loupe of 4 × magnification to prevent small prey being overlooked. Specimens with prey in their chelicerae were placed in separate vials containing 75% ethyl

alcohol and brought back to the laboratory for body length measurement and prey identification.

All spiders observed were classified into several groups according to their age, sex and presence or absence of egg sacs near females. When the investigation started, the vast majority of spiders were in the sub-adult stage. Thus, the following four groups were delimited: (1) sub-adult males, which had swelled, but not differentiated pedipalp tips; (2) adult males, with distinctly developed palpal sclerites; (3) pre-reproductive females, including all spiders without swollen pedipalp tips and without egg sacs; (4) females guarding their egg sacs. During each survey the number of spiders with and without prey was counted separately within each of the four groups. Because the study area was large (ca. 500 × 500 m) and successive surveys were conducted in different parts of this area, it is highly likely that most of the *O. globifer* observed were different specimens. The log-likelihood ratio test (G_1 statistic) was used for comparison of percentage of feeding specimens among different groups of spiders. Voucher specimens of *O. globifer* and their prey items were deposited at the Institute of Zoology, Azerbaijan Academy of Sciences.

In total, 947 specimens of *O. globifer* were observed, 52 of which (5.5%) had prey in their chelicerae. Among them 93 sub-adult males (6 with prey ~6.5%), 153 adult males (4 with prey ~2.6%), 431 pre-reproductive females (36 with prey ~8.4%) and 270 females with egg sacs (6 with prey ~2.2%) were recorded. The percentage of feeding specimens in pre-reproductive females was significantly higher than those in adult males ($G_1 = 6.98$, $P < 0.01$) and egg-guarding females ($G_1 = 12.7$, $P < 0.001$). In contrast, there was no statistically significant difference between pre-reproductive females and sub-adult males in this respect ($G_1 = 0.39$, $P > 0.5$).

One spider seen with prey escaped, so 51 prey items were collected for dietary analysis. These prey items were distributed among five orders of arthropods: four from the class Insecta (Hymenoptera 68.6% of total prey, Diptera 11.8%, Lepidoptera 11.8%, Homoptera 2.0%), and one from the class Arachnida (Araneae 5.9%). The dominant food component was worker ants, which accounted for 62.7% of total prey. *Cataglyphis aenescens* Nylander contributed the bulk of ants (28 specimens), followed by two *Cardiocondyla* sp. and two *Plagiolepis* sp. Other hymenopterans included two bees *Coelioxys argentea* Lepeletier (Megachilidae), *Halictus* sp. (Halictidae) and one parasitic wasp (Braconidae). Diptera were represented by five bombyliids (*Villa* sp.) and one dolichopodid fly, and Lepidoptera comprised one unidentified moth and five unidentified caterpillars. Among the spiders captured were one gnaphosid (*Micaria rossica* Thorell 1875), one unidentified salticid and one con-
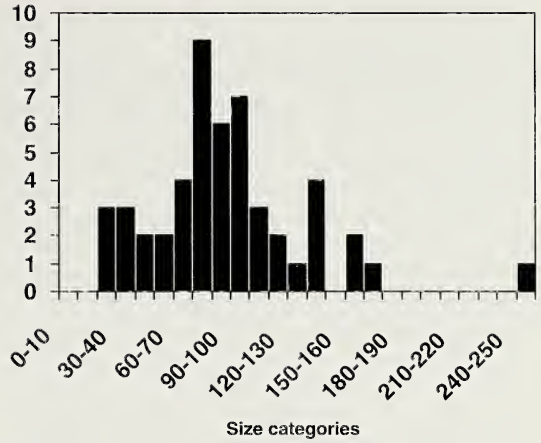

Figure 1.—Distribution of prey in different size categories, which are body lengths of prey expressed as percentage of the body lengths of their captors.

specific. The latter was the male captured by the female; i.e. sexual cannibalism probably took place. The remaining prey was a leafhopper (Cicadellidae).

Fifty prey items were measured. Their length varied from 1.5–12.8 mm (mean ± SD: 4.9 ± 2.6 mm) and constituted from 22.7–243.8% (88.8 ± 40.9%) of the length of their captors (Fig. 1), which ranged from 4.7–9.0 mm (6.7 ± 1.0 mm). According to their body length, all prey of *O. globifer* can be divided into three groups. Small prey, not exceeding 3 mm in length, made up 14.9% of total prey measured. This group included the salticid spider, the dolichopodid fly, the leafhopper, *Cardiocondyla* and *Plagiolepis* ants, none of which exceeded half the size of their captors. The largest part of the diet of *O. globifer* (62.5%) was medium-sized arthropods (3–7 mm), consisting of all specimens of *Cataglyphis aenescens*, the halictid bee, the braconid wasp, two spiders (*Micaria rossica*, *Oxyopes globifer*) and one lepidopteran larva. Relative length of these prey items varied from 50–110%. The third group consisted of arthropods larger than 7 mm, being from 110–250% of their captors' lengths. This prey amounted to 22.9% of the prey as a whole and included a moth, a megachilid bee, bombyliid flies and most caterpillars.

There was no positive relationship between spider length and prey length (Correlation analysis, $r = 0.1588$, $P = 0.271$), and no difference between spider sexes in the prey length taken (ANOVA, $F_{4,45} = 0.3020$, $P = 0.875$).

The percentage of feeding specimens in the population of *O. globifer* studied was low (5.5%), as is usual with cursorial spiders (Nyffeler & Breene 1990) and lynx spiders in particular (Nyffeler et al. 1987a, b, 1992). Moreover, the percentage of feed-

Table 1.—Length of prey of different oxyopid species.

Spider species	n	Length of spiders mm		Length of prey mm		Length of prey %		Source
		range	mean	range	mean	range	mean	
Oxyopes salticus	64	2.6–8.0	—	0.6–5.6	2.61	10.0–110.0	—	Nyffeler et al. 1987b
Oxyopes salticus	63	1.9–8.0	4.24	0.5–5.8	2.41	8.0–129.0	56.0	Nyffeler et al. 1992
Peucetia viridans	25	8.2–12.7	10.96	1.6–16.5	5.90	14.0–130.0	—	Nyffeler et al. 1987a
Peucetia viridans	31	4.5–16.5	10.08	1.3–13.6	7.04	26.0–136.0	68.0	Nyffeler et al. 1992
Oxyopes globifer	50	4.7–9.0	6.70	1.5–12.8	5.90	22.7–243.8	88.8	Present study

ing specimens among adult males was significantly lower than among pre-reproductive females. Laboratory investigations on feeding in other oxyopids have also revealed that males feed less often than females (Lingren et al. 1968; Furuta 1977). A similar tendency has been reported in jumping spiders (Salticidae) by Jackson (1977) and Givens (1978). Both investigators attributed this fact to the specific life style of salticid males, which emphasizes mating and only opportunistically involves feeding. In contrast, females, which need a high intake of food for yolk production, spend much of their time searching or waiting for prey. It seems reasonable to apply this speculation to lynx spiders too. In this context it is worthwhile to note that the percentage of feeding specimens among sub-adult males of *O. globifer* was comparable to that among pre-reproductive females. Apparently the life style of immature males does not differ significantly from that of females and changes drastically only after final molt.

After oviposition, lynx spider females normally attend their cocoons (e.g., Cutler et al. 1977). Such behavior facilitates protection of eggs and increases survival of the offspring (Fink 1986), but it is disadvantageous for parent spiders themselves, since this restricts their hunting activity. Although egg-guarding oxyopid females have been observed eating prey (e.g., Willey & Adler 1989), this is probably not frequently the case, because spiders have no opportunity to choose optimal foraging sites when they brood their egg sacs. One would therefore expect a substantial reduction in feeding frequency in *O. globifer* females during the egg-guarding period. In fact, the percentage of feeding specimens among egg-guarding females was significantly lower than among solitary ones. In wolf spiders the feeding frequency of maternal females is also significantly lower than that of non-maternal females (Nyffeler 2000).

This investigation has shown that *O. globifer* is a polyphagic predator feeding on a wide range of arthropods. Lynx spiders are generally known to have broad diets (see Nyffeler 1999). The heavy prevalence of worker ants in the diet of *O. globifer* may be unusual, since these insects, possessing effective defensive equipment, are not palatable to most cursorial spiders (Nentwig 1986). However, myrmecophagy is apparently a common phenomenon within the family Oxyopidae. Worker ants were found among the prey of all lynx spiders, where data on natural prey is available: *O. salticus* (Nyffeler et al. 1987b), *O. apollo* (Agnew & Smith 1989), *O. scalaris* (McIver 1989), *O. licenti* and *O. sertatus* (Furuta 1977), *P. viridans* (Nyffeler et al. 1992). Does *O. globifer* prefer ants to other prey or is their predominance in its diet due to the abundance of these insects on *Salsola nodulosa*? Experimental laboratory investigations are required to answer this question. However, extensive field observations on the prey of *O. salticus* in cotton agroecosystems in the USA have shown the proportion of ants in the diet of this species to be highly variable. While worker ants were the dominant food component of spiders occurring in Houston County, Texas (Nyffeler et al. 1987b), their percentage was quite insignificant in the diet of *O. salticus* inhabiting cotton fields in Burleson County, Texas (Nyffeler et al. 1992), and they were entirely missing among prey of spiders observed in Sunflower County, Mississippi (Lockley & Young 1987). These data suggest that the proportion of ants in the diets of *Oxyopes* species may depend significantly on their abundance in the spider's habitat.

The range and mean value of relative length of prey of *O. globifer* were greater than those of other lynx spiders studied (Table 1). However, this difference is not pronounced. There was a marginally significant positive relationship between spider length and prey length across species (Correlation analysis, $r = 0.853$, $P = 0.066$). Larger species (*P. viridans*) tended to catch larger prey, while smaller species (*O. salticus*) tended to catch smaller prey than did *O. globifer*.

Laboratory tests on prey-size preference of spiders have shown that most cursorial spiders do not capture prey larger than 150% of their body length, with a most preferred range of 50–80% (Nentwig & Wissel 1986). *Oxyopes globifer* caught several

prey items exceeding 150% of its length. However, the proportion of such prey in its diet was low. Moreover, only one prey item was more than two-fold larger than its captor (243.8%). This is probably the largest prey recorded for oxyopid spiders (in terms of prey/predator size ratio). All other prey have not exceeded 170% in relative length, and medium-sized arthropods prevailed among them. Thus, one can conclude that the prey-size spectrum of *O. globifer* is, in general, comparable to the common pattern found among cursorial spiders, although it is somewhat biased to large prey.

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THE FEATURES OF CAPTURE THREADS AND ORB-WEBS PRODUCED BY UNFED *CYCLOSA TURBINATA* (ARANEAE: ARANEIDAE)

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ABSTRACT. Orb-webs constructed by members of the spider family Araneidae are composed of sticky and non-sticky threads deposited in a stereotypic fashion. This study examines how changes in a spider's nutritional condition affect the capture thread properties and architectural details of its web. It does so by characterizing the features of successive webs constructed by unfed spiders that were not allowed to recycle previous webs. The volume of a capture thread's viscous material and the threads' inferred stickiness decreases in successive webs, although the capture thread's extensibility does not change. The lengths of both capture thread and non-sticky thread decrease at similar rates in successive webs. The decreasing stickiness of capture threads reduces the stickiness per unit capture area. We did not detect asymmetry in the spacing of either spiral or radial threads of first and last webs, nor did we observe differences in the sizes of viscous droplets in outer and inner spiral turns. This suggested that these spiders assessed their silk resources before they initiated web construction and altered their behavior to produce a highly regular web of an appropriate size for their silk reserves.

Keywords: Nutrition, hunger, silk allocation, spider, thread extensibility, thread stickiness

Orb-webs constructed by members of the orbicularian subclade Araneoidea are highly integrated structures formed of the products of three spinning glands that independently draw their components from a common hemolymph pool (Foelix 1996). Non-sticky threads produced by ampullate glands form the web's anchor, frame, hub, and radial threads. The spirally arrayed, sticky prey capture thread is produced by two spinning glands. The flagelliform spigot on a posterior lateral spinneret produces a supporting axial fiber and the two adjacent aggregate spigots coat this fiber with a viscous aqueous solution. Material from the two posterior lateral spinnerets merge and the viscous solution coalesces into a series of droplets. These droplets are formed of a complex solution of organic and inorganic compounds, a variety of small proteins, and high molecular weight glycoproteins (Townley 1990; Vollrath et al. 1990; Townley et al. 1991; Vollrath & Tillinghast 1991; Vollrath 1992; Tillinghast et al. 1993). Glycoprotein nodules form within each droplet and are thought to make the thread sticky (Vollrath et al. 1990; Vollrath & Tillinghast 1991; Vollrath 1992; Tillinghast et al. 1993; Peters 1995). Hydrophilic compounds in the viscous material attract atmospheric moisture to maintain the thread's water content (Townley et al. 1991; Edmonds & Vollrath 1992), which accounts for about 80% of its volume (Gosline et al. 1986).

Non-sticky thread usually comprises the greater proportion of an orb-web's total thread length. Eberhard (1988a) estimates that sticky thread typically forms 36–54% of the total length of thread in an orb-web but that it is responsible for a greater percentage of an orb-web's mass because it has a greater volume per length than does non-sticky thread. This may suggest that supplies of capture thread precursors limit an orb-web's size. However, factors such as silk gland sizes, the efficiency with which glands extract precursors from the hemolymph, and the metabolic cost of producing threads affect a spider's ability to produce threads.

Orb-web architecture results from an interaction between the spider's innate web-building behavior, the environment, and the spider's silk resources. Web features such as capture area, number of radii, and spiral spacing exhibit intraspecific plasticity (Witt & Baum 1960; Eberhard 1988a). The effects of a spider's nutritional condition may contribute to this variability. Several studies report that as spiders became heavier the spiral spacing of their web increases (Witt & Baum 1960; Christiansen et al. 1963; Witt 1963).

Poor nutrition may affect web architecture in two ways. It may limit the supply of a spider's total silk protein, thereby reducing the lengths of all web elements, or it may also limit the length of all or some web elements by restricting one or more critical amino acids or other web compounds (Higgins & Rankin 1999).

Many spiders, including the species used in this study (pers. obs.), ingest silk and sticky droplets as they take down their webs and recycle this material in the new webs they construct (Carico 1986). This improves the economy of orb-web use; estimates of reuse of organic orb-web constituents range from 32–97% (Breed et al. 1964; Peakall 1971; Townley & Tillinghast 1988). Using the most conservative of these estimates, Opell (1998) concluded that web recycling reduced the cost of orb-web construction by about 32%. If web production is limited by certain amino acids and other compounds critical for web production, then web recycling may have even greater benefits.

A spider could accommodate diminishing supplies of thread precursors in two ways (Witt et al. 1968; Eberhard 1988a): 1. Evaluate silk supplies prior to web construction and alter the design of the entire web or 2. Respond to dwindling silk supplies as they are encountered during web construction. In the first case, if non-sticky silk reserves were low, a spider might construct a smaller outer frame that would reduce web area and minimize changes in the number of radii. If capture thread reserves were low, increased spiral spacing could maintain a uniform stickiness-per-web-capture-area ratio, but would alter the web's radius-to-spiral-turn ratio. In the second case, a severe reduction in non-sticky thread during frame construction might result in more widely spaced radii. If capture thread

was being depleted, spiral spacing might increase in successive (more central) spiral turns or the size of the capture thread's viscous droplets might also decrease centrally.

To examine the effect of nutritional deficit on orb-webs and their threads, we measured the features of successive threads and webs produced by unfed spiders. Our investigation expands an earlier study (Witt 1963) by examining a different species and by measuring the web and thread features of the same spiders over time, rather than comparing the features of one group of fed spiders and another group of starved spiders. To further limit a spider's silk resources, we also removed most of the silk from a web before it could be recycled. These procedures allowed us to test the hypothesis that the length of sticky thread declines more rapidly than non-sticky thread, and to examine the influence of diminishing nutritional resources on the volume, extensibility, and inferred stickiness of viscous thread. It also permitted us to further test the hypothesis (supported by Witt et al. 1968) that a spider assesses its silk resources before beginning web construction and uses this information to alter its silk allocation and web architecture, thereby maintaining uniform spacing of web elements and conserving critical elements of web design.

METHODS

Species studied.—We studied adult female *Cyclosa turbinata* (Walckenaer 1842), collected from June to August 1999 on the Virginia Polytechnic Institute and State University campus, and surrounding areas of Blacksburg, Montgomery County, Virginia (N 37.22874, W 80.42558). At the end of the study, spiders were preserved in 70% ethanol and identified using Levi (1977). Voucher specimens are deposited in the Museum of Comparative Zoology.

Experimental design.—Whenever possible, the stabilamentum was collected along with the spider and suspended from a support in the container in which the spider was housed, as this encouraged web building (Rovner 1976). Spiders were kept in 25 × 37 × 12 cm plastic boxes set upright on their longest sides. Wooden dowel rods 5 mm in diameter were glued around the perimeter of the box to serve as web attachment sites. The side of the box opposite the lid was removed

and covered with plastic food wrap to allow easy access to the webs. The boxes provided ample space to accommodate the webs that *C. turbinata* produce under natural conditions. The boxes were kept in an environmental chamber with a 13:11 h dark-light cycle, a temperature of 25° C and a relative humidity of 80%.

We examined spiders daily and, after thread samples were collected or a web was photographed, we destroyed most of the web and removed most of its silk, leaving only the stabilamentum and a few framework lines and radii to encourage the spider to construct another web. After its web was destroyed, each spider was given an opportunity to drink by placing it on water-saturated cotton. If a spider did not make a web after 3 or 4 days, it was released.

Spiders were divided into two groups that were sampled on alternate days. Of the spiders we placed in boxes, eight produced enough webs to be included in comparisons of webs and ten produced enough webs to be included in thread comparisons. Every 48 hours, webs constructed by one group of spiders were dusted with corn starch (Carico 1977) and photographed. Uncontaminated capture threads were collected from webs produced by the other group of spiders. The webs constructed by spiders of each group were numbered sequentially. As many as 21 webs were made by individual spiders whose webs were dusted and as many as 30 webs by individual spiders whose threads were collected (mean numbers 12.4 and 13.8 respectively).

Web features.—Boxes containing dusted webs were elevated above a black cloth and the webs were photographed from a distance ~0.7 m. A reference measurement was recorded and, after printing enlarged photographs, used to compute an enlargement index for each web photograph. From these measurements, the lengths of sticky and nonsticky threads, spiral spacing, and the total area and capture area of webs were determined using the formulas given in Opell (1997).

We evaluated the regularity of spiral spacing and radial line distribution in the first and last webs constructed by the six spiders that produced the greatest number of webs. We measured the distance between the six outermost and between the six inner-most spirals

along two radii in each web. From this, the mean inner and outer spiral spacing was computed. We measured (along the same spiral turn) the distance between each of three radii to the left and three radii to the right of these two reference radii and computed mean radius spacing.

Thread features.—The features of sticky thread samples taken from the outer- and inner-most 1–4 spiral turns of a web were measured. These samples were collected by carefully placing calipers whose tips were coated with double-sided tape against a thread and then cutting this portion from the web with small scissors. From each sample, we measured the lengths and widths of two droplets from each of two different thread segments and, from the same regions of the thread, the distance spanned by a series of droplets (mean number droplets = 17.5 droplets). When droplet size differed within a segment, we measured the dimensions of one of the smaller and one of the larger droplets. From these measurements, droplet volume (μm^3) per mm was calculated using the formulas given by Opell (1997). We evaluated the regularity of viscous droplet size and spacing in the first and last webs constructed by ten spiders that produced the greatest number of webs by comparing the droplet features of their outer and inner spiral turns.

The stickiness of an adhesive capture thread can be estimated from the volume of the thread's droplets (Opell 2002). This volume is computed from measurements of droplet length, width, and distribution (Fig. 2 & Formulas 1–4 in Opell 2002). The thread measurements used to compute this volume are shown in Figure 2 of Opell (2002). We used the data from this earlier study to develop a formula to estimate the stickiness of capture threads produced by adult *C. turbinata*. This was done by regressing the volume of thread droplets per mm of thread length against thread stickiness to obtain the significant ($n = 17$, $F = 11.16$, $P = 0.0041$, $R^2 = 0.41$) formula:

Stickiness (μN/mm thread contact)

= droplet volume (μm^3) per mm

× 0.000221

+ 4.87.

Table 1.—Comparison of thread features. L_B = thread length at breaking, L_I = initial thread length. Values are reported as mean ± 1 standard error. The mean number of webs in each of the three categories is presented in the first row. The P values of repeated ANOVA's are given for the complete model and separately for the three web orders and the ten spiders whose values were included. An * denotes features that we consider to show change by virtue of significant model and order (web sequence) P values and consistently increasing or decreasing mean values.

	Webs 1–3 $n = 15$, $\overline{X} = 1.9 \pm 0.3$	Webs 4–7 $n = 12$, $\overline{X} = 5.6 \pm 0.3$	Webs 8–30 $n = 26$, $\overline{X} = 13.9 \pm 1.1$	ANOVA P Values (Model, Order, Spider)
Droplet Diameter (μm)	9.68 ± 1.00	7.17 ± 0.40	5.68 ± 0.31	* 0.000, 0.000, 0.035
Droplets per mm	38.7 ± 2.9	42.0 ± 3.6	55.5 ± 3.4	* 0.008, 0.001, 0.139
Total Droplet Volume (μm³ / mm × 10³)	17.52 ± 4.28	9.17 ± 1.79	6.71 ± 1.47	* 0.047, 0.000, 0.241
Extensibility (L_B / L_I)	4.14 ± 0.38	3.26 ± 0.34	3.86 ± 0.32	0.048, 0.563, 0.039

We then computed estimated stickiness values for each of the undusted web samples of the current study and regressed these stickiness values against the sequential numbers of the webs from which these threads were taken to obtain the significant ($n = 51$, $F = 15.26$, $P = 0.0003$, $R^2 = 0.23$) formula:

Stickiness (μN/mm thread contact)

= − 1.2742 natural log web number

+ 9.4346.

Using this formula, we assigned a stickiness value to the threads in each of the dusted webs. As these were the webs for which we measured thread lengths, this permitted us to estimate the total stickiness of the webs' capture threads and the stickiness per web capture area.

After the droplets on the threads were measured, the thread was placed on the tips of digital calipers covered with double sided tape and opened to a distance of 2.5 mm. A motor separated the tips of the calipers at a rate of 17 μm per second. When the thread broke, the motor was stopped and the distance the calipers had spread was recorded. Extensibility was then computed as a ratio of the breaking length of a thread to its initial length.

Statistical analyses.—We included in our analyses of threads only spiders that constructed at least 9 webs (mean number of webs = 13.3) and in our analysis of webs only spiders that constructed at least 7 webs (mean number of webs = 10.3). We divide webs into three sequential groups (e.g., for thread features: Webs 1–3, Webs 4–7, and Webs 8–30) and used a repeated measures analysis of variance (RMANOVA) test to examine differences among the values of thread and web features. Spiders could (and did) make more than 1 web in each of the three web groupings that we used, which is one reason we used the RMANOVA and also accounts for sample sizes being greater than the total number of spiders used. The RMANOVA model included two components: web sequence and spider. The former accounted for changes in nutritional condition and the latter for inter-individual variability. We consider as significant only those values whose increase or decrease was marked by the following: 1. a significant ($P \leq 0.05$) overall model; 2. a significant web sequence model component; and 3. a consistent (non-oscillating) change in the value in question. If, for example, the first two requirements were met but an index showed a reduction in the Webs 4–7 sequence but an increase in the Webs 8–30, we attributed this oscillation to a cause other than declining nutritional condition. Paired t-tests were used to compare spiral and radial spacing and capture thread droplet features. Statistical tests were performed with SAS for the Power Macintosh computer (SAS Institute, Cary, North Carolina).

RESULTS

Thread features.—Mean droplet diameter decreased and mean droplet number per mm increased in subsequent webs (Table 1). The net result was a decrease in droplet volume per mm of thread, with the mean value for webs in the last group being only 38% that of the webs in the first group. In contrast, thread

Table 2.—Comparison of web features. Values are reported as mean ± 1 standard error. The mean number of webs in each of the three categories is presented in the first row. When the sample size differs from that reported immediately under each of the three web sequences, this number is reported in brackets. The P values of repeated ANOVAs are given for the complete model and separately for the three web orders and the ten spiders whose values were included. An * denotes features that we consider to show change by virtue of significant model and order (web sequence) P values and consistently increasing or decreasing mean values.

	Webs 1–3 n = 9, $\overline{X}$ = 2.1 ± 0.3	Webs 4–6 n = 8, $\overline{X}$ = 4.9 ± 0.2	Webs 7–21 n = 20, $\overline{X}$ = 11.6 ± 1.1	ANOVA P Values (Model, Order, Spider)
Frame Length (cm)	552.3 ± 39.9 [8]	491.4 ± 22.0 [7]	409.9 ± 20.7 [18]	0.026, 0.065, 0.329
Radii Length (cm)	2027.0 ± 250.6 [8]	1797.1 ± 117.3 [7]	1287.1 ± 94.3 [18]	* 0.000, 0.014, 0.011
Non-capture Length (cm)	2579.3 ± 277.5 [8]	2288.6 ± 106.2 [7]	1697.0 ± 111.5 [18]	* 0.001, 0.012, 0.019
Capture Length (cm)	2026.4 ± 216.2 [8]	1662.6 ± 96.1	1273.6 ± 84.1	* 0.003, 0.006, 0.113
Total Thread Length (cm)	4684.5 ± 488.5 [8]	3958.2 ± 195.7 [7]	2937.1 ± 195.4 [18]	* 0.001, 0.007, 0.054
Radii Length/Frame Length	3.64 ± 0.4 [8]	3.73 ± 0.4 [7]	3.10 ± 0.1 [18]	0.033, 0.434, 0.047
Non-capture/Capture Length	1.24 ± 0.05 [8]	1.39 ± 0.08 [7]	1.40 ± 0.05 [18]	0.013, 0.080, 0.015
Radii Length/Capture Length	0.96 ± 0.05 [8]	1.08 ± 0.06 [7]	1.05 ± 0.04 [18]	0.003, 0.072, 0.003
Spiral Turns	25.2 ± 1.4	21.9 ± 1.2	18.9 ± 0.7	* 0.002, 0.004, 0.126
Spiral Spacing (mm)	1.73 ± 0.06	2.01 ± 0.01	2.11 ± 0.07	0.000, 0.085, 0.000
Number of Radii	45.5 ± 3.3 [8]	42.1 ± 1.3 [7]	34.4 ± 1.5 [19]	0.000, 0.073, 0.005
Radii per Spiral Turn	1.77 ± 0.09 [8]	1.97 ± 0.11 [7]	1.83 ± 0.05 [19]	0.001, 0.016, 0.000
Total Web Area (cm^2)	109.6 ± 14.3	106.0 ± 10.0	87.2 ± 7.6	0.147, 0.116, 0.171
Capture Area (cm^2)	101.2 ± 13.4	98.0 ± 9.8	80.9 ± 7.1	0.130, 0.111, 0.143
Total Stickiness (mN)	17562 ± 2116	12341 ± 702	8191 ± 588	* 0.000, 0.000, 0.111
Stickiness per Area (μN / cm^2)	179.5 ± 10.4	130.5 ± 7.6	108.8 ± 7.5	* 0.000, 0.000, 0.004

Table 3.—Indices of web regularity. The mean number of webs in each of the two categories is presented in the first row. Values are reported as mean ± 1 standard error. *P* values are for paired t-tests.

	First Web $n = 6,$ $\overline{X} = 2.0 \pm 0.6$	Last Web $n = 6,$ $\overline{X} = 11.8 \pm 2.2$
Radii Spacing:		
Right (mm)	7.93 ± 0.47	7.13 ± 0.56
Left (mm)	8.42 ± 0.40	7.31 ± 0.72
P	0.099	0.637
Spiral Spacing:		
Outer (mm)	1.95 ± 0.20	2.08 ± 0.13
Inner (mm)	1.95 ± 0.16	2.00 ± 0.14
P	0.928	0.177

Table 4.—Indices of droplet regularity. The mean number of webs in each of the two categories is presented in the first row. Values are reported as mean ± 1 standard error. *P* values are for paired t-tests.

	First Web $n = 10,$ $\overline{X} = 1.2 \pm 0.1$	Last Web $n = 10,$ $\overline{X} = 13.3 \pm 1.4$
Droplet Diameter:		
Outer (μm)	11.13 ± 1.04	5.43 ± 0.39
Inner (μm)	10.69 ± 2.39	4.56 ± 0.45
P	0.853	0.066
Droplets per mm:		
Outer	28.33 ± 3.51	51.09 ± 4.14
Inner	43.17 ± 5.88	76.35 ± 9.80
P	0.070	0.012

extensibility did not change in successive webs (Table 1).

Web features.—Although frame thread length declined during the study this difference was not significant (Table 2). However, the lengths of all other web elements diminished by 34–37% in subsequent webs (Table 2). The surprising uniformity of this decline is also documented by the failure of web order to explain differences in the ratios of radii thread to frame thread lengths, non-capture to capture thread lengths, and radii to capture thread lengths. The decline in capture thread length was reflected in a decreased number of spiral turns, although this was not accompanied by an increase in spiral spacing. The number of radii did not diminish. Total web capture area did not decrease. However, as a consequence of declining capture thread volume per mm of thread length (Table 1), total estimated web stickiness decreased by 47%. This was associated with a 32% decrease in the estimated stickiness per cm^2 of web capture area.

The spacing of radii and capture spirals showed no irregularity in first or last webs (Table 3) and, therefore, provided no evidence of diminishing intra-web silk resources. Outer spirals tended to have larger droplets that were more closely spaced than inner spirals (Table 4). However, the only significant difference was in the droplet distribution of the last webs constructed.

DISCUSSION

Cyclosa turbinata exhibited a surprising ability to continue constructing orb-webs in the absence of both new resources and recycled material from previous webs. Reduced metabolic rate induced by starvation (Anderson 1974) and the elimination of bouts of prey capture may help extend a spider's resources. The lengths of both capture threads and non-sticky threads decreased in subsequent webs, but we found no support for the hypothesis that capture thread length decreased more quickly than non-sticky thread length. It is possible that frame thread length did not decrease significantly because, when leaving web remnants to encourage spiders to re-build their webs, we may have left proportionately more non-sticky threads than sticky threads. Due to the subjectivity of this procedure, we are unable to assess this possibility. However, we believe that we left so little silk that it had a minimal effect. The maintenance of a fairly stable ratio of these two thread types may be explained by the decrease in the volume of viscous material covering the capture threads. Rather than compensating for diminishing capture thread reserves only by reducing capture thread length, *C. turbinata* reduces both capture thread length and capture thread volume. This may help explain why the observed decrease in web capture area was not significant. In contrast, in studies using *Araneus* spp., Witt (1963) found that web diameter decreased and spiral spacing increased after 10 and 17 days of starvation. The regularity of

radii and capture spirals in *C. turbinata* webs supports the hypothesis that a spider can assess its silk resources before constructing a web and, even as these resources decline, construct a web that has a regular architecture. This agrees with Witt's (1963) observations on *Araneus diadematus* Clerck, 1757. Evidence for memory based, compensatory web construction behavior has been noted in orb-web temporary spiral construction in other species (Eberhard 1988b).

The nutritional independence of the capture thread's inner axial lines and their viscous covering is shown by the thread's unchanging extensibility (attributed to its axial lines) in the face of its decreasing viscous volume (Table 1). Changes in the size and distribution of the thread's viscous droplets may result from changes in the chemical composition of this material or smaller amounts of viscous material may alter the dynamics of droplet formation. Changes in the diameters of axial fibers may also influence droplet size. As the thread's viscous material has both high water content (Gosline et al. 1986) and hydrophilic capabilities (Townley et al. 1991), a spider's hydration and the humidity of its environment may affect the features of its capture thread. We attempted to control for these factors by providing spiders with regular access to water and maintaining them and measuring their threads under uniform conditions.

Although we attribute the changes in threads and webs that we observed to the declining nutritional states of the spiders, we cannot entirely rule out the effect of aging. However, we judge the aging effects to be relatively minor as our study ended in August, and at this locality, *C. turbinata* adult females build webs until mid October. Additionally, the webs we observed were judged symmetrical by our indices and showed none of the characteristics of "senile webs" that are sometimes built by orb-weaving spiders near the end of their lives (Eberhard 1971).

ACKNOWLEDGMENTS

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CYTOGENETICS OF THREE BRAZILIAN *GONIOSOMA* SPECIES: A NEW RECORD FOR DIPLOID NUMBER IN LANIATORES (OPILIONES, GONYLEPTIDAE, GONIOSOMATINAE)

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ABSTRACT. Currently, 60 species of harvestmen have been karyotyped and all of these are from the Nearctic and Palearctic regions. This work is the first cytogenetic report of three gonyleptid species of the suborder Laniatores: *Goniosoma* aff. *badium*, *G. proximum* and *G. spelaeum* of the Neotropical region, from the southeastern region of Brazil. Conventional Giemsa stain chromosome preparations were obtained from embryonic cells and adult male testes. Embryo mitotic plates of *G.* aff. *badium* and *G. proximum* indicated 88 chromosomes, and mitotic spermatogonial plates of *G. spelaeum* males revealed intra- and interindividual variation of chromosome number, ranging from 92–109 chromosomes. In the three analyzed species, the mitotic chromosomes were meta- or submetacentric with no obvious sex chromosomes being identified during mitosis. Prophase I spermatocytes of *G. spelaeum* also revealed intra- and interindividual bivalent number variation and furthermore indicated the presence of multivalence. The karyotypes of these three *Goniosoma* species exhibited the largest chromosome pair with a negative heteropycnosis in the distal region of the shortest arm; chromosomes of *G. spelaeum* submitted to silver impregnation evidenced this negative heteropycnotic region as nucleolus organizer region (NOR). These results, when compared with cytogenetic data of other Laniatores species from the Palearctic region, indicated that a new record for diploid chromosome number probably characterize the genus *Goniosoma* in the Neotropical region.

Keywords: Chiasma, chromosome chain, karyotype, Palpatores, meiosis

Harvestmen are cosmopolitan in distribution and are grouped into three suborders: Cyphophthalmi, with about 50 sparsely distributed species; Palpatores, with about 2000 species concentrated in the Holarctic region; and Laniatores, with about 3500 mainly Neotropical species (Pinto-da-Rocha 1999).

Cytogenetic analysis of harvestmen is well documented for the suborder Palpatores with more than 50 species of Palpatores that have been karyotyped. However, the karyotype of members of the other suborders are poorly known with only two species of Laniatores and one of Cyphophthalmi that have been

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characterized. Overall in the Opiliones, diploid numbers vary from 10–78 chromosomes (Sokolow 1929, 1930; Suzuki 1941, 1966, 1976, 1980; Juberthie 1956; Parthasarathy & Goodnight 1958; Tsurusaki 1982, 1985, 1986a, 1990; Tsurusaki & Cokendolpher 1990; Cokendolpher & Jones 1991). The diploid chromosome numbers found so far in the suborder Laniatores ranged from 40 for *Pseudobiantes japonicus* Hirst 1911 (Epedanidae) to 78 for *Vonones sayi* (Simon 1879) (Cosmetidae). In contrast, Tsurusaki (1985) found the suborder Palpatores had diploid chromosome numbers varying from 10–36. The highest diploid chromosome number of 52 was observed in the manubriatum (under montanum) subgroup of the *Leiobunum curvipalpe* group,

due to the tetraploidy from specimens having 2n = 24 (Tsurusaki 1985). In Cyphophthalmi, *Siro rubens* Latreille 1804 was found to have 2n = 30 chromosomes (Juberthie 1956).

The morphology of the chromosomes in the Opiliones has been described for some Palpatores species but for only one Laniatores species. In these species, the predominant chromosomes are meta—or submetacentric (Sokolow 1929, 1930; Suzuki 1941, 1966, 1976, 1980; Juberthie 1956; Parthasarathy & Goodnight 1958; Tsurusaki 1982, 1985, 1986a, 1990, 1993; Tsurusaki & Cokendolpher 1990; Cokendolpher & Jones 1991).

The sex chromosome system has been morphologically distinguished in only 13 species of Palpatores; most of them have an XY/XX system (Suzuki 1976, 1980; Tsurusaki 1982, 1985, 1986a, 1986b, 1989, 1990; Tsurusaki & Cokendolpher 1990), with one exception, *Mitopus morio* Fabricius 1799, which has a ZZ/ZW system (Tsurusaki & Cokendolpher 1990).

All previous karyotype descriptions of Opiliones were performed in species from Nearctic and Palearctic regions. Moreover, only a few non-systematic studies were focused on Neotropical harvestmen (Ramires & Giaretta 1994; Gnaspini 1995, 1996). This paper describes the first cytogenetic study of harvestmen belonging to suborder Laniatores (Gonyleptidae, Goniosomatinae) from the Neotropical region; the study includes embryonic metaphase analyses of *Goniosoma* aff. *badium* and *G. proximum* (Mello-Leitão 1933) and analyses of testicular mitotic and meiotic cells of *G. spelaeum* (Mello-Leitão 1933). The goal of this work was to determine the karyotypes of these three *Goniosoma* species and additionally, to describe the chromosome behavior of *G. spelaeum* during meiosis.

METHODS

Cytogenetic analyses were carried out on three *Goniosoma* species from southeastern Brazil: on six embryos of *G. aff. badium* from Barragem de Guaricana (25°43'S, 48°58'W), São José dos Pinhais, PR; on eight embryos of *G. proximum* from Gruta do Moquem, PE-TAR-Parque Estadual Turístico do Alto Ribeira (24°38'46"S, 48°42'2"W), Iporanga, SP; on six adult specimens (four males and two females) of *G. spelaeum* from Gruta do Tatu (24°16 05"S, 48°25'03"W), Ribeirão Grande,

SP. All analyzed specimens were collected in November 1999.

To date, *G.* aff. *badium* has only been collected from the tunnels of the Guaricana Dam; *G. proximum* is widespread in the Atlantic Forest in the State of São Paulo, inhabiting small cave entrances and trees; *G. spelaeum* is a trogloxene species, living in the cave entrances in Vale do Ribeira, also in the State of São Paulo (Gnaspini 1995, 1996). These three species are nocturnal. Male and female vouchers specimens are deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP), São Paulo, SP, Brazil.

The chromosome preparations followed the method described by Webb et al. (1978), with some modifications. Dissected embryos and gonads were placed in insect saline containing 0.05% colchicine to arrest the metaphase cells. The hypotonic treatment was completed by adding a volume of tap water equal to that of insect saline containing 0.05% colchicine and was left for 15 min. The material was then fixed in methanolic Carnoy for 1 hour. Each embryo and/or gonadal tissue was macerated in a drop of 60% acetic acid by tapping the material with the flat end of metal rod on the slide. The slides were dried on a warm plate (~45° C) for 2 min. The preparations were stained with 3% Giemsa (1.5 ml of Giemsa stock solution, 45 ml of distilled water, and 1.5 ml of pH 6.8 phosphate buffer). Some testicular preparations of *G. spelaeum* were submitted to silver impregnation (Howell & Black 1980; Kodama et al. 1980) to determine the chromosomes bearing the nucleolus organizer regions (NORs).

The egg samples of *G.* aff *badium* and *G. proximum* indicated asynchronous embryo development and only a few embryos were suitable for cytogenetic analysis. The first cytogenetic results of *G. spelaeum* revealed variable diploid chromosome numbers, which was initially interpreted as a consequence of technical preparation problems. Considering that the loss and overlapping of chromosomes could be a result of, respectively, long and short duration of hypotonic treatments, decreasing times of hypotonic treatment were tried and also resulted in diploid number variation. Finally, the squash technique was also tried to avoid putative overspreading and loss of chromosomes of the mitotic and meiotic plates. Due to the presence of high diploid

Figures 1–3.—Karyotypes of three *Goniosoma* species stained with Giemsa: 1. *Goniosoma* aff. *badium* embryo (2n = 88); 2. *Goniosoma proximum* embryo (2n = 88); 3. *Goniosoma spelaeum* adult male (2n = 105). Arrows indicate the negative heteropycnotic region of pair 1. Scale bar = 10 μm.

chromosome number and the small size of the chromosomes, the squash technique did not allow any better resolution of the mitotic plates and also indicated chromosome number variation. Female gonads of *G. spelaeum* were also analyzed for chromosome preparations, but no cellular division was found.

Due to the high number and small size of the chromosomes, some restrictions were established to accomplish the karyotype characterization of these three *Goniosoma* species. This included considering only well spread

mitotic plates showing low numbers of over-lapped chromosomes and those having a reasonable degree of chromosome condensation to allow centromere identification.

RESULTS

The majority of embryo metaphases of *G.* aff. *badium* and *G. proximum* revealed a karyotype of 2n = 88 chromosomes (Figs. 1, 2); in a few embryo metaphase cells, the diploid chromosome number varied in the same individual or different specimens, which was interpreted as accidental gaines or losses of chromosomes among cells during slide preparation. From a total of 76 spermatogonial metaphases preparations of *G. spelaeum*, only 26 were suitable for cytogenetic analysis. The selected *G. spelaeum* spermatogonial metaphases showed intra- and interindividual variation in relation to the diploid chromosome number that ranged from 92–109 chromosomes (Table 1, Fig. 3). Considering the high chromosome number variation, the diploid number for the *G. spelaeum* was not determined. The chromosomes of these three *Goniosoma* species exhibited mainly meta- or submetacentric morphology (Figs. 1–3). Chromosomes that were differentiated by size and/or morphological heterogeneity, which could indicate sex chromosomes, were not noted in the karyotypes of the *Goniosoma* species.

A notable karyotypic feature shared by these *Goniosoma* species was the presence of a negative heteropycnosis in the distal region of the short arm of the largest chromosome pair of the karyotype (Figs. 1–4). Other differentially stained chromosome regions were also noted in these karyotypes. However, these regions did not constitute common characteristics to the three analyzed *Goniosoma* species. The identification of all these differentially stained regions depended on the degree of chromosome condensation.

Table 1.—Number of chromosomes observed in diploid cells (2n) and first meiotic metaphases (n) of four males of *Goniosoma spelaeum*.

Male number	2n					n				
	# of preps	Range	mean	mode	median	# of preps	range	mean	mode	median
1	6	92–103	97.5	96	97.5	6	39–46	42	40	40.5
2	6	93–105	96.8	97	96	7	40–47	43.6	42	42
3	5	97–100	98.6	98	98	1	43–43	43	43	43
4	9	99–101	103.1	101	101	8	44–53	47	45	45.5

Figures 4–6.—Mitotic chromosomes of *Goniosoma spelaeum*: 4. Pairs 1 submitted to Giemsa staining showing different degrees of condensation and clearly visible negative heteropycnotic regions (arrows); 5. Spermatogonial metaphase (2n = 100) stained with Giemsa; 6. The same spermatogonial metaphase showed in Fig. 5 submitted to silver nitrate impregnation, exhibiting NORs (arrows) in the pair 1 chromosomes. Scale bar = 10 μm.

Silver impregnation of Giemsa stained mitotic metaphases of *G. spelaeum* evidenced active NOR in the distal region of the short arm of the pair 1 chromosomes (see arrow in Figs. 5, 6). The NOR labeling was coincident with the negative heteropycnotic region of pair 1.

Testicular preparations of *G. spelaeum* indicated cells in pachytene and diplotene stages. Pachytene cells of *G. spelaeum* showed at least 46 filamentous structures, regular in width, which were probably formed by separated or end-to-end associated bivalents (Fig. 7); nevertheless, the exact number of associated chromosomes was impossible to determine.

Diplotene spermatocytes of *G. spelaeum* also revealed variable bivalent numbers and additionally showed the occurrence of a typical chromosome chain. The diplotene cells exhibited a maximum of 53 bivalents plus a chain (Figs. 8, 9). From 100 studied diplotene cells, only 24 permitted a count of the bivalent number and clearly showed the chromosome chain. Table 1 shows the bivalent number variation in the analyzed diplotene cells. Early diplotene cells exhibited ring multivalence (Fig. 8) and late ones showed a linear multivalence (Fig. 9). Probably the latest multivalent configuration appeared due to the precocious chiasma terminalization (Fig. 9).

Although sufficient number of diplotene cells have been analyzed, the number of chromosomes in the multivalent was not determined because the chromosomes were highly condensed, and lacked morphological resolution. Additionally, the precocious chiasma terminalization events, involving the chromosomes in the multivalent and perhaps the bivalents, allied with the high degree of chromosome condensation, also compromised the establishment of the exact bivalent number. As a consequence, some diplotene chromosome elements could not be identified as univalent or bivalent. Moreover, the type sexual determination system was not established, considering that none of the meiotic chromosome elements showed any particular feature that could permit sex chromosome recognition. Giemsa stained interphasic nuclei of *G. spelaeum* indicated several positive heteropycnotic dots, which were variable in number and probably representative of heterochromatin. Therefore, neither large nor frequent het-

eropycnotic blocks were noted in interphasic nuclei that could be interpreted as sex chromatin.

Early prophase I meiocytes and interphasic nuclei of *G. spelaeum* submitted to the silver impregnation revealed the presence of one to three blocks of nucleolar material deeply impregnated (Figs. 10–13), suggesting that there are at least one and a maximum of three active NORs. Late diplotene cells did not provide detectable labeling of nucleolar material or bivalent carrier of the NORs.

DISCUSSION

The karyological results of these three gonyleptid species are similar to *Vonones sayi* (Simon 1879) (Laniatores, Cosmetidae) in relation to the high number and morphology of the chromosomes and no obvious sex chromosomes. *V. sayi* has 2n = 78, with most of the chromosomes being metacentric or submetacentric (Cokendolpher & Jones 1991). However, the high chromosome numbers observed in these species that belong to the suborder Laniatores, contrast with those described for most of the species of Palpatores, whose diploid chromosome numbers vary from 10–36 (Tsurusaki 1986a; Tsurusaki & Cokendolpher 1990).

In comparison to the total number of species of Opiliones, only a small percentage have been karyotyped, and those are members of Laniatores. In considering the cytogenetic data described for Cyphophthalmi, Palpatores, and Laniatores species, the *Goniosoma* species karyotype differentiation seems to have occurred by an increase of the chromosome number. Probably chromosomal centric fissions followed by pericentric inversions were responsible for the chromosome number increase and meta- or submetacentric morphology maintenance of the *Goniosoma* species.

Using phylogenetic analyses based on mor-

←

rows indicate linear chromosome association; 8. Diplotene cell with approximately 45 bivalents plus a ring multivalent (large arrow). The small arrows indicate a bivalent with interstitial and terminal chiasmata; 9. Late diplotene cell with about 47 bivalents plus a linear multivalent (arrowhead). The medium size arrow indicates a bivalent with one interstitial chiasma. Scale bar = 10 μm.

Figures 7–9.—*Goniosoma spelaeum* prophase I cells stained with Giemsa: 7. Pachytene cell with approximately 45 filamentous structures. The ar-
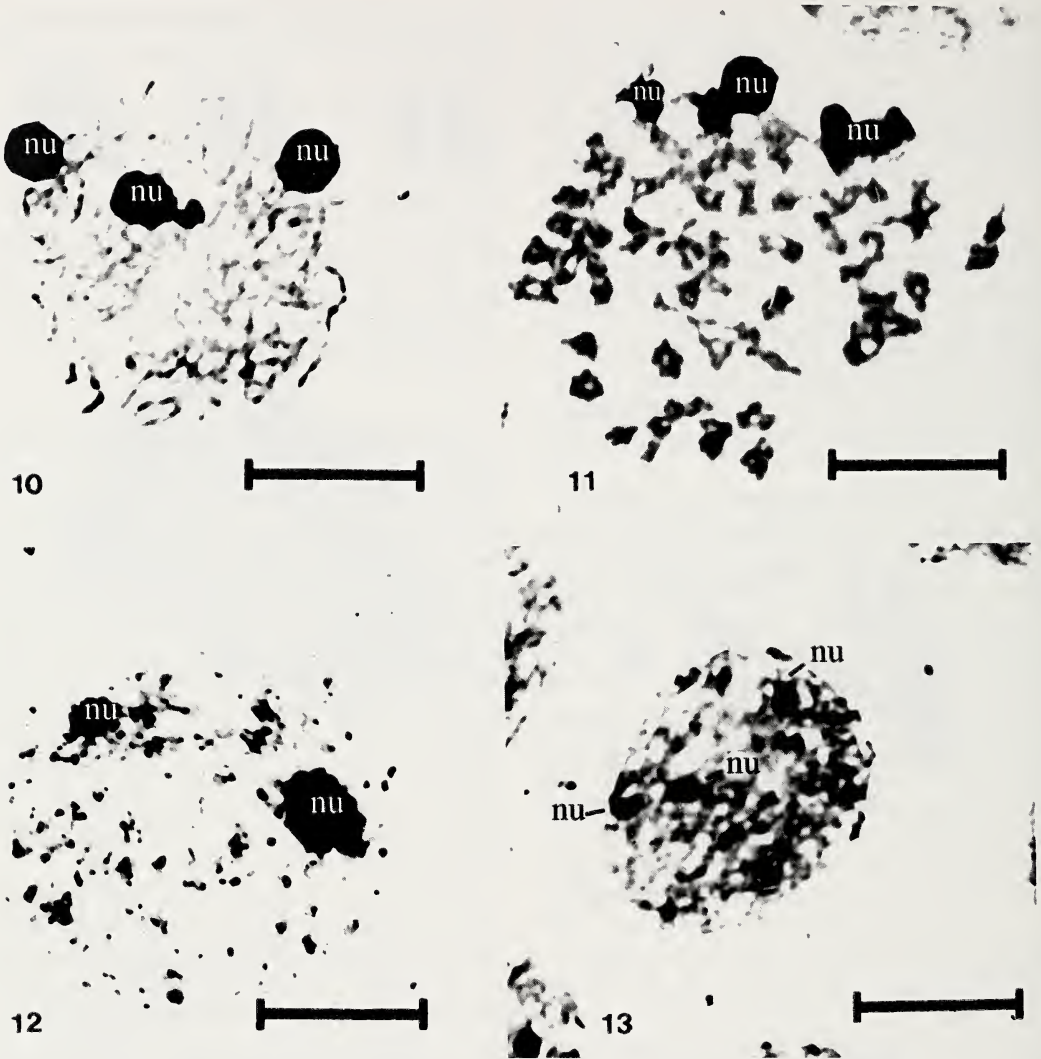
Figures 10–13.—Prophase I and interphasic nuclei of *Goniosoma spelaeum* submitted to silver nitrate impregnation: 10,11. Early prophase I and diplotene nuclei, respectively, both exhibiting three blocks of nucleolar material (nu); 12,13. Interphasic nuclei, showing respectively, two and three blocks of nucleolar material (nu). Scale bar = 10 μm.

phological and molecular data from several species belonging to Cyphophthalmi, Palpatores, and Laniatores, Giribet et al. (1999) found that Gonyleptoidea (Laniatores) includes species with highly derived characteristics. This differs from other species of the Laniatores superfamily. These data corroborate the possibility of the *Goniosoma* species having a highly derived karyotype.

The diploid number variation noted in the *G. spelaeum* testes cells could be a consequence of differential chromosome non-disjunction, involving heterozygous chromo-

somes for translocation or supernumerary chromosomes, or random gaines or losses of chromosomes among cells during the procedures of chromosomal preparations.

The variation in intra-individual chromosome number is not common, but there are descriptions about its occurrence in some species that possess heterozygous specimens for structural chromosome rearrangements (Ohno et al. 1965; Beçak et al. 1966; Hartley & Horne 1984; Thode et al. 1985; Giles et al. 1985). This intra-individual variation seems to be a consequence of somatic chromosome

non-disjunction that could favor the reconsti-tution of homozygous chromosomes. The chromosome non-disjunction presumably functions as an "accumulation mechanism" and is particularly evident in some polymor-phic species for supernumerary chromosomes (White 1973; Gorlov & Tsurusaki 2000a, b; Tsurusaki & Shimada 2004).

The presence of supernumerary chromo-somes, which are extra chromosomes, in Op-iliones is well documented in *Psathyropus tenuipes* Koch 1878 (formerly *Metagagrella tenuipes* Suzuki 1949) (Tsurusaki 1993; Gor-lov & Tsurusaki 2000a, b; Tsurusaki & Shi-mada 2004). This species showed extensive variation in the number of chromosomes, ranging from 0–19, among cells of a single individual and among individuals of a single population, as well as among populations. They behave as univalents during meiosis, though some of them seem to form a chain with end-to-end associations in diakinesis (Gorlov & Tsurusaki 2000b).

The *G. spelaeum* multivalence was identi-fied in all prophase I cells analyzed, but this feature does not constitute an accurate param-eter to determine if these chromosomes are or are not supernumeraries. The description of multivalent-like associations between super-numerary chromosomes during meiosis are rare in the literature (Jones & Rees 1982; Gor-lov & Tsurusaki 2000b).

The *G. spelaeum* meiotic multivalent con-figurations suggest the occurrence of hetero-zygous chromosomes for serial translocations. Although pachytene filaments with special configurations, such as loops or open crosses, are indicative of heterozygosity for structural chromosome rearrangements, these were not seen in the analyzed cells, probably due to the occurrence of heterosynapsis. The *G. spe-laeum* multivalent configuration is similar to that found in *Delena cancerides* Walckenaer 1837 (Araneae), *Neotermes fulvescens* (Sil-vestri) 1901 (Isoptera) and *Keyacris scurra* (Rehn) (Orthoptera), which arose from hetero-zygous and serial interchanges, such as centric fusions and reciprocal translocations (Rowell 1985, 1991a, 1991b; Hancock & Rowell 1995; Martins & Mesa 1995; White 1973).

In Opiliones there is only one description about NORs in *Psathyropus tenuipes* (=*Me-tagagrella tenuipes*) (Gorlov & Tsurusaki 2000b). In this species, the NOR was associ-ated with a single A-chromosome. Although this species has an XY-XX sex chromosome system (Tsurusaki 1993), whether this single NOR is on one of the sex chromosomes in unclear. In *G. spelaeum*, the NORs were as-sociated with the largest pair, which could possibly be sex chromosomes. In Palpatores harvestmen species, whose sex determination system has already been established (Tsuru-saki 1985, 1989, 1990, 1993; Tsurusaki & Cokendolpher 1990) the X and Z sex chro-mosomes displayed similar size to the largest chromosomes of the diploid complement.

Considering the range of nucleolar material observed at interphase and prophase I, it is likely that more than two NOR-bearing chro-mosomes might be present, since activation or inactivation mechanisms in these regions could be playing a role on the gene transcrip-tion.

This work characterized three species of Brazilian harvestmen *G.* aff. *badium* (2n = 88), *G. proximum* (2n = 88) and *G. spelaeum* (2n = 92–109). These species showed a high chromosome diploid number and several meta- or submetacentric chromosomes. The results suggests that chromosomal evolution in the genus *Goniosoma* occurred by an in-crease of chromosomal number through cen-tric fissions, which were followed by pericen-tric inversions. *G. spelaeum* evidenced both intra- and interindividual variable diploid numbers which could be explained by the presence of translocated chromosomes in het-erozygous. The presence of multivalents dur-ing meiosis in this species corroborates the hypothesis of occurrence of heterozygous chromosomes for serial translocations.

ACKNOWLEDGMENTS

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NEPHILA HIRTA, A NEW SYNONYM OF EUSTALA FUSCOVITTATA (ARANEAE, ARANEIDAE)

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ABSTRACT. *Nephila ?hirta* Taczanowski 1873 was described from French Guiana, but is currently listed under *Nephilengys* L. Koch. It is here redescribed and transferred from Nephilinae (Tetragnathidae)* to the araneid genus *Eustala* Simon, and proposed as a junior synonym of *E. fuscovittata* (Keyserling 1864). *Eustala* appears to be the most speciose American araneid genus and is in need of revision.

Keywords: *Nephila, Nephilengys,* Nephilinae, Tetragnathidae, Araneidae, taxonomy, French Guiana

Taczanowski (1873) described *Nephila ?hirta* from Cayenne, French Guiana. Roewer (1942) placed the species in *Nephilengys* L. Koch 1872, where it currently remains (Platnick 2005), *contra* Bonnet (1958) who retained it in *Nephila* Leach 1815. Taczanowski's description of both sexes is sufficient to establish that the species is neither a nephiline nor a tetragnathid* [NB: the male syntype is immature]. Our examination of the types confirmed the need for a taxonomic transfer.

Museum abbreviations: ANSP = Academy of Natural Sciences, Philadelphia, U.S.A.; BMNH = Natural History Museum, London, UK; CAS = California Academy of Sciences, San Francisco, USA; MCZ = Museum of Comparative Zoology, Cambridge, Massachusetts, USA; PAN = Muzeum i Instytut Zoologii, Polska Akademia Nauk (Polish Academy of Sciences), Warsaw, Poland; USNM = Smithsonian Institution, Washington, DC, USA.

TAXONOMY

Family Araneidae Simon 1895
Genus *Eustala* Simon 1895

Eustala Simon 1895: 795; Levi 1977: 96; Levi 2002: 532, 550.

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Type species.—*Epeira anastera* Walckenaer 1842 by original designation.

Diagnosis.—Simon (1895) diagnosed *Eustala* by the anteriorly projecting epignal scape, among other features (Simon 1895: 796): "*Uncus vulvae brevis et acutus antice directus.*" Levi (1977) revised the 13 species north of Mexico including the type species, *E. anastera* (Walckenaer). He confirmed Simon's epignal diagnosis (Levi 1977: figs. 118, 138, 140; see also Figs 1, 3) and added the diagnostic feature of the male palp, notably a protruding white cone-shaped median apophysis (Levi 1977: figs. 126, 147, 232-m). The type species is also illustrated in Levi (2002: figs. 13–15).

Systematics.—Simon (1895) placed *Eustala* in the group Mangoreae within Argiopinae (equivalent to Araneidae). In a cladistic study by Scharff & Coddington (1997), *Eustala* is sister to the doublet *Wixia* O.P.-Cambridge 1882 plus *Acacesia* Simon 1895 within the subfamily Araneinae, but that relationship depended on a single homoplasious synapomorphy. Their study used genera as terminals and so did not include genus-level autapomorphies, but *Eustala* has two (the anteriorly-directed scape and cone shaped median apophysis) that would likely plot as synapomorphies of the genus.

Diversity.—For the 89 currently deemed valid *Eustala* species (all American) more
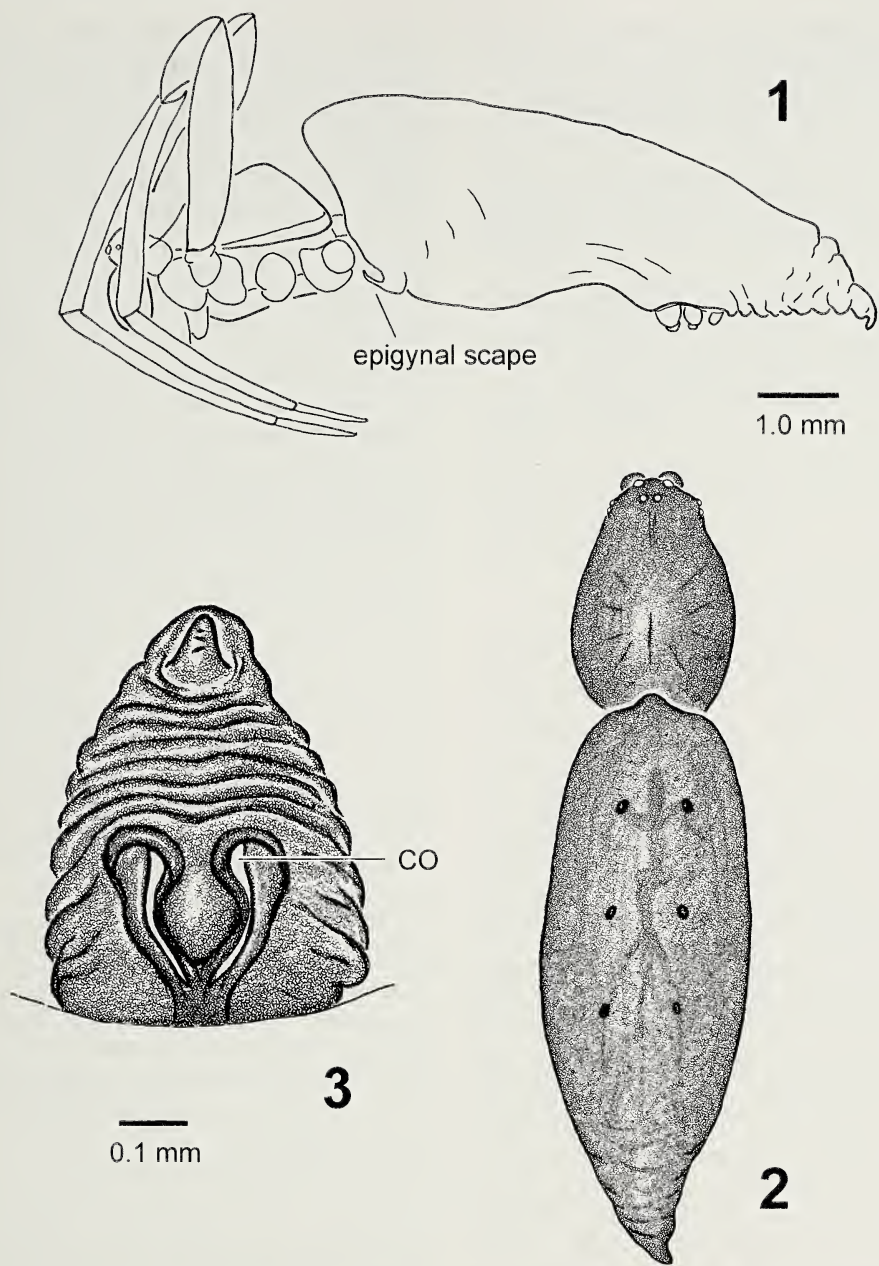
Figures 1–3.—*Eustala fuscovittata* (Keyserling), female from Cayenne, French Guiana (syntype of *Nephila hirta* Taczanowski): 1. Lateral view (note the epigynal scape projecting anteriorly); 2. Dorsal view; 3. Epigynum, ventral view. CO = copulatory opening.

than 100 names are available (Platnick 2005). *Eustala* seems to be the most speciose neotropical araneid genus (H.W.L. pers. obs.). It is in need of revision. For example, a recent inventory of spiders of southern Guyana found four sympatric species in a single rain forest hectare (Kuntner pers. obs., specimens in USNM). Although likely to be new, none of these can be currently identified without original descriptions and type specimen examination. A further impediment in *Eustala* taxonomy is the difficulty to diagnose species

morphologically, and the potential for apparent hybridization (H.W.L. pers. obs.).

Eustala fuscovittata (Keyserling 1864)
Figs. 1–3

Epeira fusco-vittata Keyserling 1864: 129, pl. 6, figs. 7–8; Keyserling 1893: 251, pl. 13, fig. 187.

Nephila ?hirta Taczanowski 1873: 149. NEW SYNONYMY.

Cyclosa thorelli McCook 1894: 228, pl. 19, fig. 11. Synonymy by F.O.P.-Cambridge 1904.

Epeira caudata Banks 1898: 255, pl. 15, fig. 5. Synonymy by F.O.P.-Cambridge 1904.

Eustala fuscovittata: F.O.P.-Cambridge 1904: 505, pl. 48, figs 3–4, ♀ ♂; Grasshoff 1970: 216, fig. 2a–c, ♀ ♂.

Nephilengys hirta: Roewer 1942: 934; Platnick 2005.

Eustala fusco-vittata: Chickering 1955: 398, figs. 1–5, ♀ ♂.

Nephila hirta: Bonnet 1958: 3073.

Types and comments.—*Epeira fusco-vittata:* female holotype from Santa Fé de Bogota, N.-Granada [Bogota, Colombia, 04°15′N, 74°11′W] (BMNH), examined by H.W.L.

Nephila ?hirta: 1 female, penultimate male, juvenile syntypes from Cayenne [04°56′N, 52°20′W] and Saint Laurent de Maroni [05°30′N, 54°02′W], French Guiana (PAN), examined. The original handwritten label reads: "*Nephila hirta* Taczanovski, Cayenne—Guyane françoise, leg. K. Yelski, detm. WT. Taczanovski". A newer typed label reads: "PAN, *Nephila hirta* Taczanowski, ♀ PARALECTOTYPES = *Eustala*, design. Levi 1970. GUYANE FRANC. Cayenne, K. Jelski". With the latter label H.W.L. indicated the need of the transfer to *Eustala*. The syntypes are poorly preserved with most legs missing or softly attached. The female genital morphology of the only adult syntype (Figs 1–3) justifies synonymy with the widespread American *E. fuscovittata*.

Cyclosa thorelli: female holotype from Key West, Florida, USA [24°33′N, 81°46′W] (from Marx collection, thus locality uncertain) (ANSP).

Epeira caudata: female holotype from Tepic, Baja California, Mexico (CAS, probably destroyed). Locality uncertain, as there does not seem to be a Tepic in Baja California.

Description.—Female syntype of *Nephila hirta* (Figs 1–3). Habitus elongate, pale yellow (in alcohol). Total length 9.9 mm. Prosoma oval, with narrow cephalic region, highest in posterior thoracic region (Figs 1–2). Prosoma 3.1 mm long, 2.1 mm wide. Lateral eyes widely separated from the medians, almost juxtaposed. Posterior median eyes separated by one diameter. Posterior median eyes with a fully median canoe tapetum as in all poorly preserved specimens, not displaced [Scharff & Coddington (1997) report displacement as araneid feature in freshly preserved specimens]. Chelicerae narrow, with four promarginal and three retromarginal teeth, cheliceral furrow denticulate. Sternum longer than wide: 1.3 mm long, 0.9 mm wide, with slight paired elevations adjacent to first and third coxae. The two preserved legs with numerous tibial and metatarsal and few femoral spines. Leg I 13.1 mm long (femur 3.3 mm; patella 1.6 mm; tibia 3.1 mm; metatarsus 3.1 mm; tarsus 1.0 mm). Opisthosoma elongate, cylindrical, extends beyond spinnerets (Figs. 1–2). Opisthosoma 7.3 mm long, 2.8 mm wide. Posterior median spinnerets with an extensive aciniform spigot field. Epigynum with a wrinkled, anteriorly projecting scape and ventral, conspicuous copulatory openings (Figs. 1, 3). *Male:* For descriptions, see Keyserling (1893), O.P.-Cambridge (1904), Chickering (1955) and Grasshoff (1970).

Note added in proof.—Since the acceptance of this paper, Kuntner (2005, 2006a, b) has presented phylogenetic analyses, which dispute the tetragnathid placement of nephilines, and elevate the clade (*Clitaetra* (*Herennia*(*Nephila*+*Nephilengys*)) to family rank, Nephilidae (see also Kuntner, 2006c). Accordingly, Platnick's (2006) catalogue lists *Nephilengys hirta* in Nephilidae.

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CAUTION, WEBS IN THE WAY! POSSIBLE FUNCTIONS OF SILK STABILIMENTA IN *GASTERACANTHA CANCRIFORMIS* (ARANEAE, ARANEIDAE)

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ABSTRACT. We tested three hypotheses concerning the function of stabilimenta in the orb weaver *Gasteracantha cancriformis*: 1) warning to large animals that might accidentally destroy the web; 2) prey attraction; and 3) camouflage. One prediction of the warning hypothesis (but not of the others), that less exposed webs should have fewer stabilimentum tufts, was verified: very few tufts occurred on the peripheral lines of small webs. On the other hand, a prediction of the prey attraction hypothesis, that webs with more stabilimentum tufts should also have more captured prey, was only confirmed in one sub sample, and further analysis indicated that spider size rather than number of stabilimentum tufts best explained the presence of prey. An additional observation not in accord with prey attraction was that resting webs, which lacked sticky silk for prey capture, nevertheless had abundant stabilimentum tufts. Finally, the number of stabilimentum tufts was lower in the webs of white (as opposed to yellow or orange) spiders, contradicting a prediction of the camouflage hypothesis. The strongest conclusions from our results are support for the warning function, and lack of support for the prey attraction function.

RESUMEN. Pusimos a prueba tres hipótesis concernientes a la función de los estabilimentos en la araña *Gasteracantha cancriformis*: 1) advertencia a animales grandes que podrían destruir accidentalmente la red; 2) atracción de presas; y 3) camuflaje. Se cumplió una predicción de la hipótesis de advertencia (pero no de las demás) de que las redes menos expuestas deberían presentar menos estabilimentos: se observaron muy pocos estabilimentos en las líneas periféricas de redes pequeñas. Por otra parte, la predicción de la hipótesis de atracción de presas, de que redes con más estabilimentos deberían presentar más presas capturadas, sólo se cumplió en una submuestra y análisis posteriores mostraron que el tamaño de la araña y no el número de estabilimentos explicó mejor la presencia de presas. Otra observación que no apoya la hipótesis de atracción de presas fue haber encontrado redes de descanso, las cuales carecieron de un espiral de captura, con un importante número de estabilimentos. Finalmente, el número de estabilimentos fue menor en las redes de arañas blancas (en relación a las amarillas o las anaranjadas), contradiciendo la predicción de la hipótesis de camuflaje. Nuestros resultados apoyan la hipótesis de advertencia y no la de atracción de presas.

Keywords: orb webs, silk stabilimenta, spiders, warning, prey attraction, camouflage

The function of silk stabilimenta on the webs of diurnal orb-weaving spiders has long been debated (e.g., Hingston 1927; Marson 1947; Marples 1969; Edmunds 1986) and remains controversial (see summary by Her- berstein et al. 2000; Eberhard 2003). The hypotheses which are currently best supported include prey attraction, camouflage from predators, and web advertisement to warn off large animals which might damage the web (several

other hypothesized functions, such as providing shade for the spider, a path for the male to find the female, physical stabilization of the web, and a deposit of excess silk have little support at present). Most of the recent debate regarding silk stabilimentum function has centered on the stabilimenta in the genus *Argiope*, but silk stabilimenta have also evolved independently in several other lineages of orb weavers (Scharff and Coddington 1997; Herberstein et al. 2000). Evidence from other groups is likely to be useful in understanding possible functions.

The araneid orb weaver *Gasteracantha cancriformis* (Linneaus 1767) is widespread in the New World, ranging from the southern USA to northern Argentina (Levi 1978). Bright body colors have been said to attract prey in another species of *Gasteracantha* (Hauber 2002). It is highly variable in color and shape (Levi 1978). The orbs of mature females of *G. cancriformis* occur in fairly open situations, up to more than 6 m above the ground, and are relatively large: anchor lines extend up to 2–4 m from the hub to supports, and the diameter of the area covered by the viscid spiral can be up to 0.6 m (Marples 1967; Muma 1971).

Stabilimenta apparently evolved independently in this group (Gasteracanthini) from other araneids such as *Argiope* (Herberstein et al. 2000). The stabilimenta on *G. cancriformis* webs consist of multiple short tufts of white silk. Most tufts are on the frame and anchor lines, though they also occur on one or more radii near the hub (Comstock 1967; Marples 1967; Muma 1971; Levi 1978). Tufts of stabilimentum silk are added to frame and anchor lines while the spider is reinforcing a line already in place (Marples 1967); the spider pauses, pulls a loose swath of white silk from its spinnerets with strokes of its hind legs, dabs its spinnerets to the line one or more times to attach the swath, and then moves on. Each tuft consists of many fine threads. Newly made stabilimentum tufts blow out to the side of the main thread in the wind (thus indicating that the lines in the tufts are under no stress, and unlikely to provide any physical support for the web). The stabilimentum silk tends to stick to or entangle itself with the line, and becomes less conspicuous as time goes by (Marples 1967). Marples (1967) noted that sometimes when a spider lacks a "complete"

web (presumably an orb with a sticky spiral) it rests at a central point where several threads bearing tufts converge. Comstock (1967) speculated that the tufts of *G. cancriformis* might deceive midge-eating insects, which in their efforts to capture the supposed midges accidentally fly into the web. Muma (1971) stated (probably somewhat imprecisely, as will be shown below) that the "webs of immatures are different from those of sub-adult or adult females in lacking . . . distinct tufts of silk on the radii or foundation lines . . . "

In this note we test predictions made by each of the three major hypotheses for stabilimentum function. The warning hypothesis (but not the others) predicts that stabilimentum tufts should be more abundant in orbs which are larger and span larger spaces, and are thus under greater risk of being destroyed by large animals passing by. The fact that birds have been seen to actively avoid orb webs (Blackledge & Wenzel 1999), and that birds which have flown through spider webs show signs of intense discomfort, immediately preening themselves extensively (Robinson & Robinson 1976), support the assumption of this hypothesis that visual signals from spiders or their webs might be used by birds to avoid webs. The prey attraction hypothesis (but not the others) predicts that spiders with more stabilimenta should be more often found feeding on prey. Finally, the camouflage hypothesis (but not the others) predicts that spiders whose abdomens are white and which thus match the color of the stabilimenta (in contrast to yellow or orange, colors which also occur in the same population), should produce more stabilimenta.

METHODS

On 20 January 2004 (early dry season) in a plantation of African oil palm (*Elaeis guineensis*) located near Parrita, Costa Rica, we followed transects defined by lines of palm trees, covering an area of about 1500 m². We measured the following variables in easily accessible spider webs (approximately 1–2.5 m above the ground): 1) Spider size: estimated by multiplying the length (cephalothorax plus abdomen) by the maximum width of the abdomen (mm); 2) Maximum radius of the viscid spiral: the maximum distance between the center of the hub and the outer border of the viscid spiral; 3) Maximum span of the web:
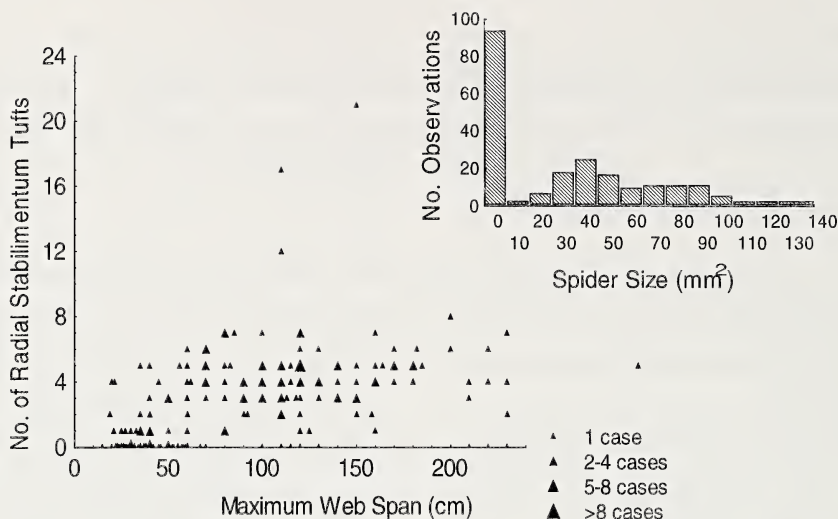
Figure 1.—Number of radial stabilimentum tufts in relation to the maximum web span. The frequency histogram at the upper right shows the distribution of spider sizes ($n = 220$).

the maximum distance between points where anchor lines were attached to the substrate; 4) Number of radial stabilimentum tufts: the number of tufts of silk on radial lines inside the viscid spiral; 5) Number of peripheral stabilimentum tufts: the number of tufts of silk on peripheral and anchor lines, i.e. all tufts outside the viscid spiral; 6) Prey: silk-wrapped prey near the hub; and 7) Color: the color of the dorsal surface of the abdomen, classified as white, yellow or orange. Although there was a certain overlap in some colors, like light yellows, it was relatively easy to assign all spiders to one of these three categories. We measured 220 capture webs with spiders, and in addition, 7 resting webs that lacked viscid spirals.

RESULTS

Warning Hypothesis.—As predicted, smaller webs had smaller numbers of stabilimentum tufts. The numbers of radial and peripheral stabilimentum tufts were positively correlated with both the maximum viscid spiral radius (R's $= 0.70$ and 0.77 respectively; $P < 0.001$ in both cases; $n = 218$) and maximum span of the web (R's $= 0.62$ and 0.76 respectively; $P < 0.001$ in both cases; $n = 220$) (Figs. 1, 2). Similarly, webs that completely lacked peripheral stabilimentum tufts were smaller than those that had them (3.6 ± 2.0 cm vs. 11.3 ± 4.7 cm for maximum radius of viscid spiral; 43.6 ± 24.2 cm vs. $111.0 \pm$

54.9 cm for maximum span; Mann-Whitney U-Test: $U = 1008$ and 1232 respectively; $P < 0.001$ in both cases; $n_1 = 71$, $n_2 = 147$).

Interpretation of these patterns is complicated by the correlations between spider size and web size, and thus the possibility of indirect effects. Small spiders had fewer radial and peripheral stabilimentum tufts than large spiders (Mann-Whitney U-tests: $U = 894$ and 424 respectively; $P < 0.01$ in both cases; $n_1 = 94$, $n_2 = 126$). Smaller spiders were also more likely to not have any stabilimentum tufts (median $= 0$ for both radial and peripheral tufts; min–max $= 0$–5 and 0–30 respectively), while the large spiders typically had a few radial stabilimentum tufts, and a larger number of peripheral stabilimentum tufts (median $= 4$ and 24.5; min–max $= 0$–21 and 0–62 respectively).

The agreement with the predictions of the warning hypothesis was not due, however, to secondary effects of the correlation between web size and spider size. When we performed partial correlations of the total number of stabilimentum tufts with the maximum span of the web, the maximum radius of the viscid spiral, and spider size, the maximum span had the highest correlation coefficient ($R = 0.35$, 0.25, and 0.16 respectively; $t_{214} = 5.51$, 3.81, and 2.42 respectively; $P < 0.01$ in all cases).

Prey Attraction Hypothesis.—In general, spiders with prey in their webs had higher
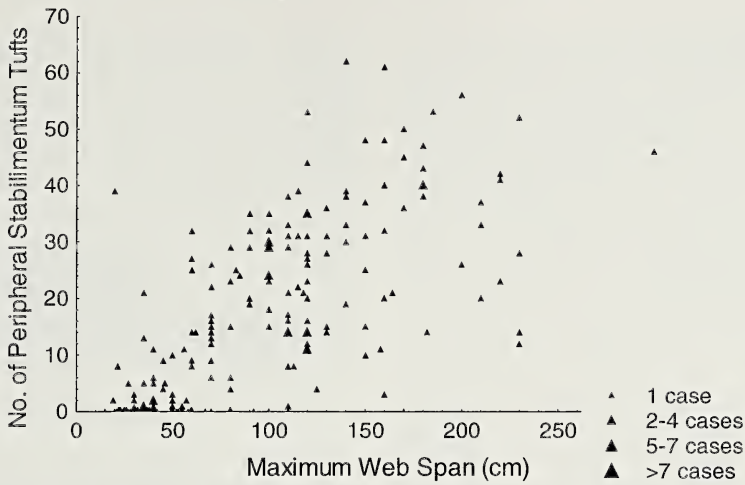
Figure 2.—Number of peripheral stabilimentum tufts in relation to the maximum web span.
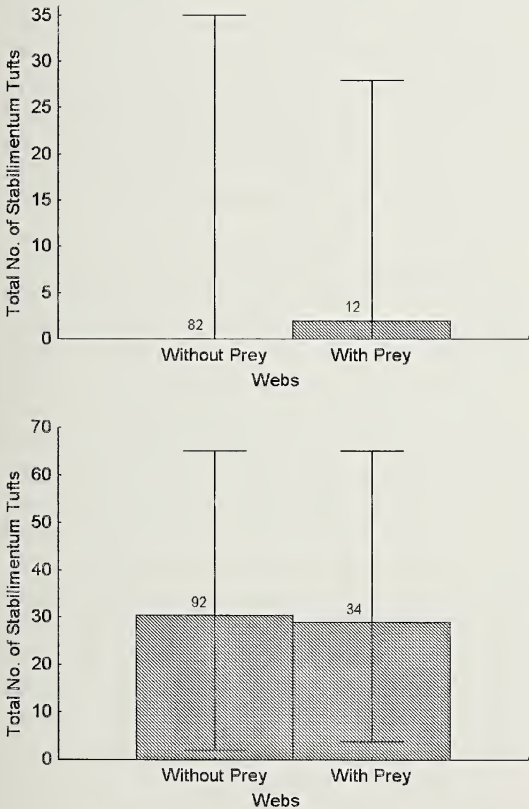
Figure 3.—The median numbers of stabilimentum tufts in webs of small (<15 mm²) and large spiders (>15 mm²) with and without prey (minimum and maximum values are represented by whiskers). Sample sizes are above the columns.

numbers of radial and peripheral stabilimentum tufts than spiders without prey in their webs (Mann-Whitney U-test: $U = 3222$ and 2939; $P = 0.036$ and 0.005 respectively). Because the array of potential prey is probably different for small and large spiders, and because the distribution of spider sizes (inset in Fig. 1) suggested the separation of spiders in two size categories (small < 15 mm², and large > 15 mm²), we repeated this analysis separately for both categories.

When the webs of small spiders with prey were compared with those of small spiders without prey, the number of radial stabilimentum tufts was not different (Mann-Whitney U-test: $U = 392$; $P = 0.26$), but the numbers of both peripheral and total stabilimentum tufts were higher in webs with prey ($U = 269$ and 272, respectively; $P = 0.01$ in both cases; $n_1 = 12$, $n_2 = 82$). On the contrary, in large spiders the numbers of radial, peripheral and total stabilimentum tufts did not vary between webs with and without prey ($U = 1508$, 1538 and 1556; $P = 0.76$, 0.88 and 0.97, respectively; $n_1 = 34$, $n_2 = 92$) (Fig. 3).

The higher number of prey in the webs of small spiders that had more stabilimentum tufts could have been an indirect effect of the relationship between the number of stabilimentum tufts and web size (which is likely to affect capture success) (see Figs. 1, 2), or between stabilimentum tufts and spider size (which is proportional to both web size and to the strength of silk lines (Craig 1987)) (Fig. 4) rather than to the stabilimenta themselves.

a)

b)
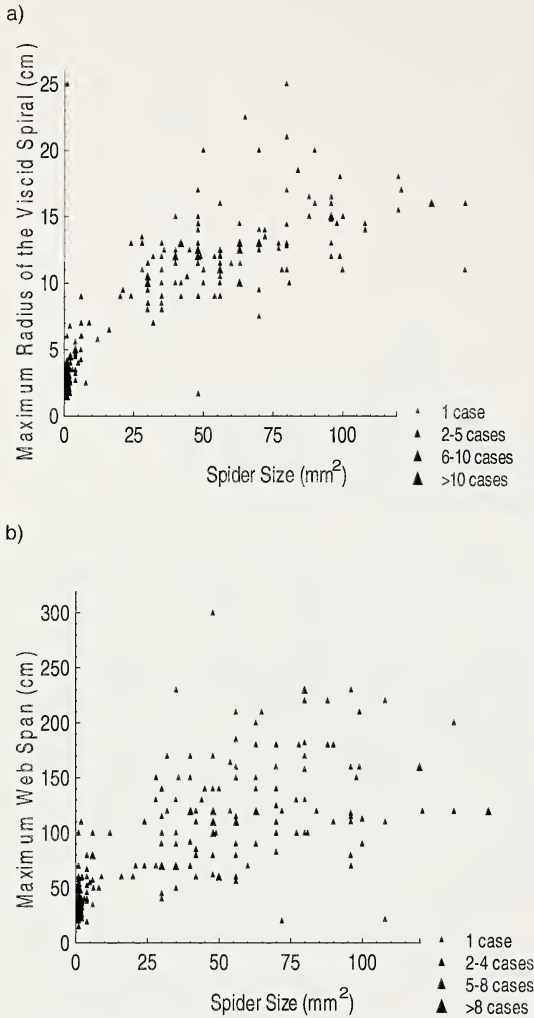
Figure 4.—Relation between maximum radius of the viscid spiral (a) and maximum web span (b) with spider size (Rs = 0.86 and 0.78 respectively; P < 0.001 in both cases; n_a = 218, n_b = 220).

In an effort to separate these possible effects, we performed a logistic regression using presence/absence of prey as the response variable, and the number of radial stabilimentum tufts, the number of peripheral stabilimentum tufts, spider size, maximum radius of the viscid spiral, and maximum span of the web as the independent variables. In small spiders, the spider size was the only variable to explain prey presence (Final loss = 33.23; X^2 = 5.3 and P = 0.021), while in large spiders prey presence was not explained by any of the variables.

We also found seven spiders (44.3 ± 34 mm² in size) on "resting" webs. These were relatively small (maximum span 72.1 ± 30

Figure 5.—Median numbers of stabilimenta in webs of spiders with different colors (minimum and maximum values are represented by whiskers). Sample sizes are above the columns.

cm), had few radii, and completely lacked viscid spirals. Contrary to expectations of the prey attraction hypothesis, they all had many stabilimentum tufts (23.4 ± 17.1). In these resting webs, the number of stabilimentum tufts did not correlate with spider size (Rs = 0; P = 1), or the maximum span of the web (Rs = 0.36; P = 0.42). Spider size was also not related to the span of the web (Rs = 0.53; P = 0.22).

Camouflage Hypothesis.—The number of radial stabilimentum tufts did not vary among differently colored spiders (Kruskal Wallis (KW) test: $H_{(2.220)}$ = 5.1; P = 0.078). Contrary to the prediction of the camouflage hypothesis, the number of peripheral and total stabilimentum tufts was lower in white spiders than in yellow or orange individuals (KW: $H_{(2.220)}$ = 10.4 and 9.1; P = 0.005 and 0.010 respectively) (Fig. 5). Smaller spiders were more likely to be white, so we repeated this analysis for small and large spiders separately. This eliminated all significant differences with respect to spider color (small KW: $H_{(2.94)}$ = 0.9; 0.9 and 0.6; P = 0.64; 0.64 and 0.75 respectively; large KW: $H_{(2.126)}$ = 1.3; 1.4 and 1.0; P = 0.52; 0.51 and 0.60 respectively).

DISCUSSION

Warning Hypothesis.—The strong positive correlations of the number of stabilimentum tufts with the maximum web span and the viscid spiral radius are in accord with the prediction of the advertisement hypothesis. Her-

berstein et al. (2000) claimed that the warning function is unlikely in the stabilimenta of *Gasteracantha* because the spiders build their webs in "shrubs and understory where birds are unlikely to fly through and damage the web" (p. 665). Both our observations and those of previous authors (Comstock 1967; Marples 1967; Muma 1971) show that this characterization of *G. cancriformis* web sites is incorrect. Nor is it likely to be true for the African *Gasteracantha* species (*G. curvispina*) that builds apparently similar stabilimenta and on which they apparently based their description (they cite it in their table as building "under bushes"). The complete description from the reference they cite for this species (Edmunds & Edmunds 1986) is "The web was spun in open spaces, between or under bushes, or attached to buildings" (p. 78).

It is worth noting that the number of peripheral stabilimentum tufts increased approximately linearly with maximum web span (Fig. 2). Use of such a linear increase rule may be the mechanism by which spiders produced the adjustment in numbers of stabilimentum tufts in larger webs that was predicted by the warning hypothesis. In contrast, radial stabilimentum tufts differed in being generally lower in number and in increasing less sharply with web size (Fig. 1). If stabilimenta serve as warning devices, the peripheral stabilimentum tufts may mark the edges of the area occupied by the web, while the radial stabilimentum tufts may simply mark which side of the well-marked periphery of the web is to be avoided (because it has the dense array of radial and sticky lines). This could explain the lower numbers of radial stabilimentum tufts and their weaker relation to web size that were observed.

It is also interesting that the stronger and stickier silk lines of larger spiders that a bird would contact if it flew into an orb are probably more disturbing than the silk lines of smaller spiders, as they may be more restrictive and more difficult to clean off. So, if birds learn from experiences with webs and distinguish those made by spiders of different sizes, larger spiders should gain a greater advantage from having peripheral stabilimentum tufts. This gives a second reason under the warning hypothesis for expecting more stabilimentum tufts on the webs of larger spiders, such as we found.

Prey Attraction Hypothesis.—Our results give little support for the prey attraction hypothesis. First, given that all spiders need to feed, under this hypothesis all spiders should present stabilimenta. The fact that the majority of small spiders did not have stabilimenta in their webs is not easily explained by the prey attraction hypothesis unless *ad hoc* modifications are added. For instance, the prey attraction hypothesis could explain the reduction of stabilimenta in small webs if the prey utilized by large spiders but not by small spiders are attracted to stabilimenta, or if the cost-benefit balance (cost of predator attraction vs. benefit of prey attraction) is different for small vs. large spiders. We know of no evidence favoring these ideas, nor do we know of any data suggesting that they are incorrect.

Second, we did not find the expected relation between prey and number of stabilimentum tufts. In webs of larger spiders there was no significant relation. In small spiders we found the predicted correlation between higher numbers of peripheral stabilimentum tufts and prey, but when the analysis took into account the possibility of indirect influences of other variables, the only variable that explained prey presence was spider size. This implies that the effect on prey attributed to the number of stabilimentum tufts in small spiders may have been due to a relation between prey capture and spider size. It is important to note, however, that the arrival of prey is probably highly stochastic, so larger sample sizes than ours might be needed to document prey capture effects.

A third, especially strong type of evidence against the prey attraction hypothesis comes from resting webs. These lacked viscid spirals, and thus did not function to capture prey, but were nevertheless well equipped with stabilimentum tufts. Stabilimenta were also observed on webs that were apparently of this type by Marples (1967). These resting webs strongly suggest that stabilimenta are not used to attract prey. If these webs serve as molting platforms (one newly molted individual was observed with its shed cuticle on one of these webs, Eberhard pers. comm.), the presence of stabilimenta even on these relatively small webs could be explained by the warning hypothesis. The impact of a large animal might be especially dangerous to a spider in its relatively defenseless condition around the time

of molting. This consideration makes the presence of well developed stabilimenta on resting webs even more difficult to explain under the prey attraction hypothesis, as the impact of prey could also be dangerous for the spider. The prey attraction hypothesis could be saved from these problems by *ad hoc* adjustments (e.g. the stabilimenta on resting webs are selectively disadvantageous "mistakes" by the spider).

Camouflage Hypothesis.—Our data did not support the camouflage hypothesis, nor did they speak strongly against it. The prediction was that the white stabilimentum tufts should have been more abundant in the webs of those individuals that were more likely to be confused with them (white spiders). The lower number of stabilimentum tufts in webs of white spiders contradicts this prediction. However, the logic of this test depends on the spider's ability to adjust its behavior in terms of its own color. Even though some thomisids may be capable of this type of adjustment (Foelix 1996), we know of no case in which an araneid has been shown to be able to sense its own color. This test also depends on the colors detectable by potential predators; for some animals the white silk tufts may appear different from the white coloration of the spider. Because of these uncertainties, we conclude that our data do not justify a certain rejection of this hypothesis.

The camouflage hypothesis might explain the reduction of stabilimenta in small webs, if large but not small spiders have predators that are fooled by stabilimenta. We know of no evidence that supports this possibility. The only predator of *G. cancriformis* that we documented was the wasp *Sceliphron* sp. (Sphecidae). One nest had 3–4 cells full of adult and subadult *G. cancriformis* females. The camouflage hypothesis is compatible with the presence of stabilimenta on resting webs.

In summary, the strongest conclusions from our evidence support for the warning hypothesis, and rejection of the prey attraction hypothesis. Future studies addressing web destruction frequency and prey capture success could help test these conclusions.

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THE PREY ATTACK BEHAVIOR OF *ACHAEARANEA TESSELATA* (ARANEAE, THERIDIIDAE)

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ABSTRACT. The attack behavior of the cobweb spider *Achaearanea tesselata* (Keyserling 1884) is roughly separated into three sequential steps: descend from the suspended retreat, pass through the sheet threads, and wrap the prey from underneath the sheet. The position and speed as the spider descended varied apparently according to prey type. In the fastest descent, *A. tesselata* fell free upside down, with all legs free and stretched upward. Two other relatively slow types of descent occurred when spiders approached the sheet head down or climbing down on a mesh thread. The behavior used to pass between the sheet lines showed little variation. It occurred at high speed with the legs folded dorsally; when the legs were in this position the spider offered a very small area of impact, apparently permitting the femora to penetrate or open a space between the lines of the sheet. The spider then opened the femora of the legs to create enough space for the cephalothorax, and seizing the sheet from underneath with legs I, II, and III, the spider pulled the abdomen and hind legs through the sheet. Then the spider rushed to the prey, flung viscid lines at the prey, and wrapped it. Attacks occurred in as little as 0.11 s after the spider began its descent.

The design of the webs of *A. tesselata* transmits information regarding the location of the prey trapped on the sheet to reach the resting spider inside the retreat. The first response of the spider in her retreat was to turn to face the prey; the spider then climbed down along mesh threads following a nearly straight line to the prey.

Keywords: Cobweb spider, prey capture, orientation, web use, tangle web, silk

The design of both a spider's web and its attack behavior are likely complementary and together affect prey capture success (Eberhard 1990). Webs generally trap and partially immobilize prey (Chacón & Eberhard 1980; Nentwig 1982), but usually prey escape unless the spider further immobilizes them (Eberhard 1990). Therefore, prey capture success is partially determined by the speed with which the spider reaches the prey, which in turn is probably largely dependent on the information the spider receives regarding prey location in the web (Biere & Uetz 1981). The speed and complexity of attack behavior may be at least partially related to the web design (Eberhard 1990), since some webs may impose some restriction on the spider's movements.

Achaearanea tesselata (Keyserling 1884) is relatively common in bushes in urban areas and highly disturbed vegetation throughout its distribution in Central and South America (Levi 1959; Eberhard 1972). The web of this spider consists of a finely-spun horizontal sheet, with a dense mesh above and a few support lines below (Fig. 1, Eberhard 1972). A curled leaf, tiny twigs, small dried flowers, or other debris serve as the spider's retreat in nearly all webs. The spider rests upside down within the retreat, which is suspended near the middle of the upper mesh. The web of *A. tesselata* works as a knock down trap for flying and jumping insects. Insects that strike the upper mesh fall down onto the sheet where they are attacked by spiders. Jörger and Eberhard (pers. comm.) suggested that lines in the mesh of *A. tesselata* could also offer information to spiders regarding prey location in the web. The design of this web is apparently shared by two other species in the genus: *A. disparata* Denis 1965 (Darchen 1968) and *A. japonica* (Bosenberg & Strand 1906) (= *Theridium japonicum*). However, *A. tesselata* seems to be unique in resting above the sheet and passing through it to attack prey (Eberhard 1972).

According to Eberhard (1972), the first response of *A. tesselata* to prey in its web was

Figure 1.—Web of *A. tesselata*: notice the upper mesh (solid arrow) and the sheet (dotted arrow).

to descend from the retreat. Passing rapidly through the sheet without causing any apparent damage, the spider rushed directly to the prey wrapping and/or biting it. Considering the high density of threads in the sheet (Eberhard 1972; Jörger & Eberhard pers. comm.), it is puzzling how the spider passes so rapidly through the sheet and how this structure suffers no apparent damage. In this paper we describe in detail how *A. tesselata* descends from the retreat and passes through the sheet and discuss the advantages and possible evolution of this behavior. Furthermore, we test the hypothesis that the upper mesh lines give information regarding prey position on the sheet to the spider.

METHODS

Field observations.—Observations on attack behavior of *A. tesselata* were made in the field, from March to September 2004, within the campus of the Universidad de Costa Rica, San Pedro, San José Province, Costa Rica (9°54′N, 84°03′W; elevation 1200 m). Attack behavior of *A. tesselata* occurs so rapidly that the spider's descent and details of its movements as it passes through the sheet cannot be distinguished with the naked eye. Thus, in addition to field observations, we video recorded the complete attack sequence of 37 adult females of *A. tesselata* in the field; each individual was recorded from one to four times, giving a total of 52 sequences. Video recordings were made with a digital video camera

(Sony DCR-VX 1000) that recorded 30 frames/s.

Detailed descriptions of attack behavior are based on video analyses. Drawings are based on digital-video images imported into a computer using the program iMovie, version 2.0. Different portions of the spider were not always in focus, hence sample sizes for different analyses differed. Descriptions are all based on samples of at least 10 individuals, sample sizes lower than 10 are indicated in the text.

Density of sheet threads.—We estimated the density of threads in sheets of five webs of adult females by counting the number of threads crossing the diameter of the 1.82 mm field of view of a sample on a glass microscope slide under a compound microscope. Threads were counted from 10 to 15 fields of view in each of the five sheets and then the average number of threads per millimeter was calculated. Samples from the sheets were collected on slides framed with strips of double-sided adhesive tape (1.5 mm thick × 2.5 mm wide). Slides were carefully lifted from below the web into the threads of the sheet; the threads extending beyond the slide were cut so that only threads adhering to the tape were collected. This method allows observation of threads without modifying their original arrangement. Additionally, on each of these slides, we randomly selected 10 sheet lines of approximately 10 mm long. Along each selected line, thread connections and number of

threads crossing over, but not attached to the line were counted in 10 fields of view (0.45 mm each). The width and length of the cephalothorax and abdomen were also measured on 30 adult females of *A. tesselata* for comparison with thread density of sheets (14 from the collection of the Museo de Zoología, Universidad de Costa Rica, and 16 used in a prey location experiment). Voucher specimens of spiders have been deposited in the Museo de Zoología, Universidad de Costa Rica.

Experiments on orientation and descending speed.—Sixteen mature females with retreats and egg sacs were each placed on a three-dimensional wire structure with six extensions projected downward, forming a hexagon, hanging from a thin fishing line at 2 m above the floor. The fishing line makes it difficult for the spiders to escape upward as they cannot climb it. They frequently descend, but usually at about a meter they turn back if they have not encountered an object below. The retreats in the webs of these spiders were small enough to allow observations of the movements of the spider inside. After one or two nights spiders had spun a complete web with the sheet approximately following the hexagonal shape of the three-dimensional structure.

To determine the orientation of the spiders during the attack behavior, we dropped *Drosophila* sp. flies on the sheets of the finished webs and video recorded the spider's movements in the retreat and its orientation as it approached the prey. To video record spider's movements the camera was fixed to a platform with the lens at 10 cm above the retreat and aligned perpendicular to its top. Before each attack, we randomly selected one of the six sections of the approximately hexagonal sheet on which the prey was to be dropped. Each spider was recorded only once. We applied a binomial analysis to evaluate if the attack approach of the spider was random with respect to the six segments of the sheet. More precise measurements of the attack orientation of the spider were obtained from video records; specifically we obtained the difference in degrees of the approaching direction of the spider to the prey and prey position in the sheet. We compared the mean differences between approaching direction and prey position using a random distribution of means. This distribution was constructed under the assumption that the attack direction of spiders was random, hence the deviation from the prey position could vary from 0° (no deviation from prey position) to 180° (maximum deviation from prey position). We used a Monte Carlo Analysis (Statistica package, version 5.0) to produce 500 random samples of possible deviation angles. The mean of departure angles of *A. tesselata* was compared with a distribution of random means using a one sample Student's t-test. We complemented the information obtained in the laboratory with field observations on spiderlings and adult female orientation.

We also measured the time a spider spent in descending from the retreat to the sheet and the attack time from the retreat to the moment the attack of the prey began. Time was estimated from the video records of different spiders using a frame (30 frames/s) as a time-reference unit. Times were compared among descent and prey types using one way ANOVAs. Velocity of descent was calculated for 15 webs in which a house fly or a blow fly of similar size was dropped in the center of the sheet. The descent time was estimated in all cases from the video records and the distance from the retreat to the sheet was measured to calculate the velocity. We also calculated the free fall velocity by dropping two recently dead mature females. These spiders were frozen until dead, and then allowed to thaw. We next dropped and recorded the falling time for each spider from a platform placed at 5.5 cm above a landing surface; we repeated this three times for each spider.

RESULTS

Orientation in retreat and mesh.—The first response of *A. tesselata* in the retreat to a *Drosophila* dropped onto the sheet was to turn to orient facing "toward" the same sector of the sheet. The orientation movements of spiders in the retreat occurred in all 16 trials conducted in the laboratory: four times prey was in front of the spider, six times it was lateral to her, and six times behind her. While descending to *Drosophila* prey, spiders climbed down along the mesh lines, following a nearly straight line. In 15 out of 16 times the spider moved to the 60° section of the sheet on which a prey was dropped ($P <$ 0.0001, Binomial test). The average angle deviation of spiders to prey location at arrival to the sheet was 7.0° (8.2). This small deviation
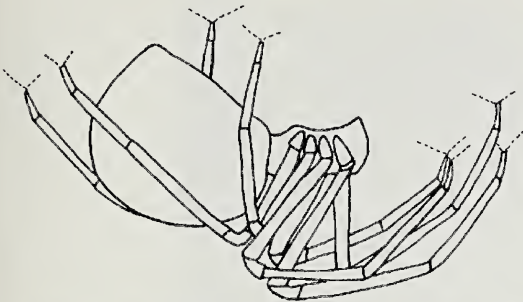
Figure 2.—Resting position of *A. tesselata* in a retreat; retreat was not drawn to show the position of the legs (dash lines indicate the possible position of threads from which the spider hangs).

is significantly smaller than a random mean (87.6 ± 48.51; $t = -9.87$, $df = 15$, $P < 0.0001$). The lines on which *A. tesselata* descended probably intersected several other threads, since the upper mesh in the web is relatively dense and lines are interconnected, but the spiders continued apparently selecting the lines running more directly toward the prey. We could not, however, see the lines in most cases. On three occasions we could see that the spider paused briefly at an intersection of lines; she briefly jerked the threads with her legs I, and then moved on the line that ran most nearly toward the prey.

In the field we video recorded the orientation behavior of three fourth or fifth instar juveniles on their mother's web. The spiderlings were on threads about three centimeters to the side and two centimeters below the retreat when a *Drosophila* was dropped on the sheet 5 cm away on the opposite sector of the sheet. The spiderlings did not descend directly to the sheet, but walked directly toward the prey through the mesh, passing under the retreat.

Position in the retreat.—The spider hung inside the retreat (if present; Fig. 2), above the sheet, where several threads converged from the mesh. The longitudinal plane of the spider formed an angle of 30° (SD ± 6°, $n = 3$), relative to the sheet, with the cephalothorax directed downward, and dorsum facing the sheet (Fig. 2). Given the position of the legs, it is likely that *A. tesselata* hangs from at least four or five different threads while in the retreat.

Descending behavior.—The position of the body and legs when *A. tesselata* came down from the retreat, after a prey falls on the sheet, varied between individuals and within the same spider depending on prey type, and possibly on hunger and experience of the spider. Relatively large flies (e.g., house flies) released the fastest reaction from the spider, provoking a very fast descent to the sheet (Table 1). Treehoppers, of about the size of a housefly, evoked a relatively slow descent; similar reactions were elicited by *Drosophila*. The variation fits relatively well into three categories: free fall, head-down, and walking on mesh threads.

Free fall: The spider fell rapidly while upside down (dorsum toward the sheet) with all legs apparently directed upward. Falls were so rapid (52.3 cm/s, SD = 13.8, range = 30.3–80.0; Table 1) that the spider was generally a blur in the video (Figs. 3–6). The spider frequently bounced when her body first struck the sheet, but sometimes passed through on first contact. When this type of descent occurred, hind legs apparently did not contact the dragline. The falling speed of dead spiders measured in the laboratory was similar to the speed calculated for spiders in the field (54.1 cm/s, SD = 5.6). However, field data may be affected by wind currents, which reduce the speed, and by different weights of spiders. In addition, the spider was apparently capable of directing her descent toward the prey position as she fell. The Figures 3–6, obtained from a

Table 1.—Average time (standard deviation in parentheses) spent by *Achaearanea tesselata* descending from the retreat to the sheet web and attacking prey. Time of attack includes from the moment the spider initiates its descent to the moment the attack begins. Information is separated by descent type; units in seconds.

	Descent type					
	Free fall ($n = 21$)		Head down ($n = 10$)		Walking ($n = 15$)	
Descent	0.11	(0.02)	1.36	(0.65)	4.08	(3.46)
Attack	1.54	(1.42)	4.64	(5.41)	5.86	(5.45)
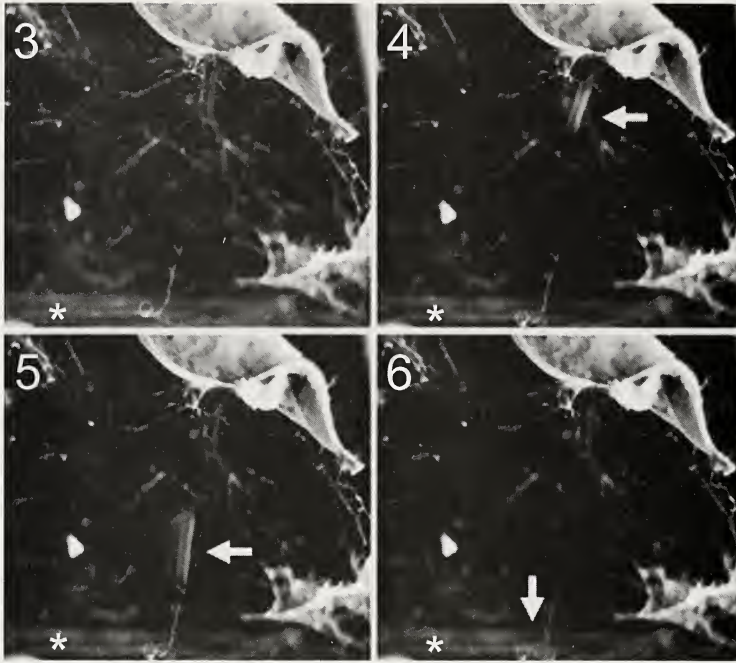
Figures 3–6.—Sequence of events during the free fall descent of *A. tesselata*. 3. The spider inside the retreat. 4. The spider beginning to fall (blur indicated by the arrow). 5. Note that the spider is only a blur due to the descent speed (arrow). 6. Point where spider struck the sheet (arrow). Note the angle of falling direction of the spider toward the left of the picture where the prey contacted the sheet (indicated by a star).

video record taken in the lab to avoid wind currents, shows how the spider oriented her fall toward the prey position (left-inferior corner of the picture). From video records, it was not possible to obtain information on how such orientation was attained by falling spiders.

Head down: The spider advanced more slowly toward the sheet maintaining a more or less head-down position (Table 1, Figs. 7–8). The spider advanced in short jerks: it first extended the anterior and second pair of legs forward and, waving them, possibly grabbed some mesh threads and moved downward a short distance. This sequence was repeated several times until the spider reached the sheet. In this descent the spider moved almost perpendicularly to the sheet through the mesh, possibly using its lines as "the steps of a ladder". During this type of descent the spider alternated the leg IV that held the dragline.

Walking on mesh threads: A. tesselata approached the sheet by walking directly toward the prey along one or a few mesh threads. In this descent the spider's body was oblique rel- ative to the sheet plane. While walking, the spider moved forward and alternately extended her anterior legs, while one leg IV held the dragline. This type of descent was much more frequent when prey fell near the edge of the sheet.

Crossing through the sheet threads.— The spider passed her body through the sheet threads with a series of extraordinarily rapid movements of legs and body that enabled her to ease her relatively large body (Table 2) through the small spaces between the sheet lines (Table 3). The movements of the spider were so rapid that it was necessary to use 32 video records of attack behavior to assemble the complete sequence of movements as the spider passed through the sheet. In all cases, independently of how she arrived at the sheet, the spider passed this structure dorsal side first. Hence, when the spider descended either head down or walking along mesh threads, she repositioned her body before passing through the sheet. In these cases, when the spider was nearly touching the sheet, she extended her first legs and grabbed a sheet line

Figure 9.—Ventral view of *A. tesselata* pulling sheet lines with her first legs. Note most of the other legs directed backwards and grabbing mesh threads to possibly counteract the forward tension exerted by pulling sheet threads.

Figures 7–8.—Position and movements of the legs of *A. tesselata* in a head-down descent. 7. Extending legs I–II and waving them to grab some mesh threads. 8. Movement of legs as the spider descended a short distance.

dragged forward, indicating that the tension was counteracted by tension on mesh threads held by the other legs, which were directed backward, except one hind leg that was in contact with the dragline (Fig. 9). From this position, *A. tesselata* released all but the first legs at once, falling in a very fast movement (ca. 0.03 s), dorsum against the sheet (Figs. 10–11).

Independently of how the spider descended from the retreat, as she passed through the sheet, her legs were tightly folded against the body, forming a compact structure that likely

with each one (Fig. 9), and then pulled these threads toward her body by folding the first legs. The sheet threads she had grabbed were bent toward the spider's body, but she was not

Table 2.—Length and width of abdomen (Ab) and cephalothorax (Cph) in millimeters for 30 mature females of *Achaearanea tesselata*.

	Ab length	Ab width	Cph length	Cph width
Average	3.1	2.3	1.8	1.4
S. D.	0.39	0.23	0.10	0.07
Range	2.6–3.7	2.0–2.6	1.7–2.0	1.3–1.5
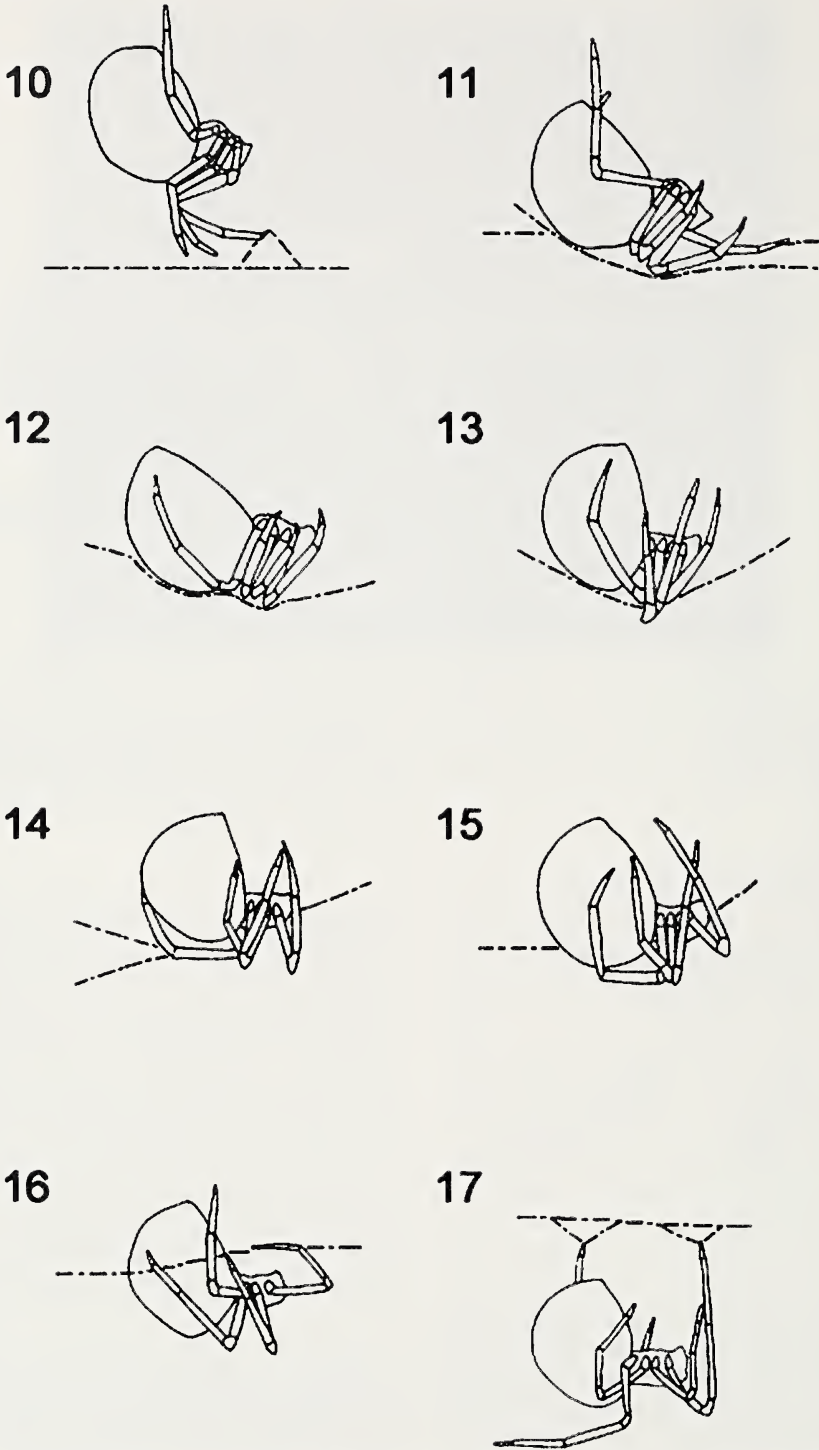
Figures 10–17.—Sequence of movements and position of legs of *A. tesselata* passing through the sheet. (Lines represent the approximate position of the sheet; threads grabbed by spider's legs in 10 and 18 were clearly observed in the video records. All legs were not always drawn when video images were not focused or angle did not allow a clear view). 10. The spider falling on the sheet after releasing its grasp on mesh threads. 11. The spider contacting the platform as she falls, note how legs began to fold on the cephalothorax. 12. The platform is deformed by the impact of the spider, the legs of the spider are tightly folded

Table 3.—Average of attachment points and unattached lines crossing over along 10 randomly selected lines in five different sheets; counts were obtained in 10 fields of view (0.45 mm each) per sheet. Mean density of sheet lines per mm calculated as number of lines across 10 to 15 fields of view (1.82 mm each) for five different sheets.

	Attachment points	Unattached lines	Density
Average	1.15	1.60	1.96
S. D.	0.61	0.80	0.59
Range	0.58–2.16	1.08–3.00	0.52–3.85

facilitated penetration between the dense woven threads of the sheet (Fig. 12; Table 3). Femora (and possibly coxae and trochanters) of legs I, II, and III of both sides were directed dorsally over the cephalothorax, nearly touching the anterior surface of the abdomen. The femur-patella joints touched or nearly touched each other and the more distal segments were pointed ventrally with tarsus and metatarsus (possibly for legs I and II) bent over the cephalothorax (Fig. 12). The femora of legs IV were approximately parallel to the others, but the more distal segments of these legs were directed backward and pressed against the sides of the abdomen (Fig. 12); one leg IV held the dragline.

The spider struck the sheet with the folded legs resting against the cephalothorax first, while her abdomen was bent upward at an angle of 30° (SD = 5°, $n = 3$; Figs. 11–12). As the spider contacted the sheet, femur-patella joints of possibly all legs were apparently pushed through a space between the sheet threads (Fig. 13). Then, the femora of all legs began to stretch out laterally, widening the space between threads of the sheet to permit the cephalothorax to pass through (Fig. 14–15). During some of these movements the distal segments of legs IV were maintained apparently immobile and pressed against the abdomen, which was still above the sheet

(Figs. 12–13). Then the spider grabbed some sheet threads from underneath with legs I, II, and III and pulled herself downward, pulling and freeing first the legs IV (Fig. 16), which grabbed some lines as soon as they passed through the sheet. The spider continued pulling, by stretching the legs ventrally, and dragged the abdomen through the sheet and then hung with some legs free (Fig. 17) before rushing toward the prey. In a few occasions, the spider showed some difficulty dragging the abdomen through the sheet so that she had to struggle to free her abdomen from the lines. The entire process of passing through the sheet took from 0.03 to 0.20 s (mean = 0.10, SD = 0.06, $n = 12$).

Capturing and transporting prey.—As soon as the spider was hanging from the sheet lines, she rushed directly to the prey that rested on the sheet. With the prey at reach, the spider began the attack by flinging lines with large viscid globs up onto it with her fourth tarsi (Griswold et al. 1998). Immediately after the first attack, *A. tesselata* started wrapping the prey, pausing frequently to either bite it or clean the tarsi of legs IV, whereas the other legs grabbed sheet lines from below. When a large prey was fully wrapped, the spider rapidly broke some sheet threads, attached a dragline by pressing the spinnerets to the prey and pulled it up to the retreat with a fourth leg, climbing up along a mesh line. The dragline was frequently attached half way to the retreat, and the spider climbed down by the same line, completely releasing the prey from the sheet threads, wrapping the prey with a few more lines, and attaching another line, pulled up the prey closer to the retreat. This procedure was repeated until the prey was at about 1 cm from the retreat. If the prey was small, the spider directly carried it up nearby the retreat with one hind leg. Occasionally, a prey escaped before the spider reached it ($n = 6$). In such cases, spiders returned to the retreat passing back upward through the sheet.

←

on the cephalothorax, except distal segments of legs IV that are pressed against the sides of the abdomen. 13. Joints femur-patella-tibia of all legs passing through the sheet. 14. Femora begin to stretch out, opening enough space to seize the cephalothorax through the sheet. 15. Femora widely stretched. 16. Most legs grabbing sheet threads from underneath, the abdomen half way passing the sheet. 17. The spider hanging from the underside of the sheet.

The process was slow and clumsy. The spider introduced different legs into different spaces between the sheet lines, making it difficult to pass through. Usually she only succeeded after several attempts, and cut and broke some lines before getting free.

Time spent during the descent and attack.—The time the spider spent descending from the retreat to the sheet was determined by how the spider approached the sheet. The average time that the spider spent in a free fall descent was significantly lower than the time she spent in a head down or walking descent ($F_{2,43}$ = 17.48, P < 0.0001; Table 1). Accordingly, the mean time from the moment the spider began her descent until the moment the attack (attack time) of the prey began was significantly lower when she fell free from the retreat ($F_{2,43}$ = 5.29, P < 0.01). However, differences in attack time are primarily related to the lower time of free fall descents, since the time the spider lasted from the moment she contacted the sheet to start attacking the prey did not differ among spiders using different descent types ($F_{(2,38)}$ = 1.74, P = 0.19).

The type of prey apparently determined how the spider descended from the retreat to the sheet. For example, free fall was more frequent when prey were blow flies or house flies, walking along lines when prey were drosophilids, and head down descents were more frequent when prey were treehoppers (χ^2 = 42.4, df = 4, P < 0.0001).

Prey entangled in mesh lines.—Occasionally a prey was entangled in mesh lines at about the same level of the retreat (n = 4). When this occurred the spider descended, passed through the sheet, and shook it from underneath, apparently trying to determine the prey's location. After a few seconds the spider climbed through the sheet into the mesh. The movements as she climbed in the mesh were clumsy and her orientation toward the prey imprecise, compared with the rapid and precise movements when locating prey on the sheet.

DISCUSSION

Horizontal aerial sheets with mesh above and/or below have independently evolved in a wide variety of separated spider groups (Shear 1986; Eberhard 1990). In some families (e.g., Linyphiidae) the spiders run upside down on the lower surface of the sheet (Bristowe 1958; Griswold et al. 1998; Benjamin et al. 2002; Benjamin & Zschokke 2004), but in other families (e.g., Lycosidae, Pisauridae) the spider runs on top of the sheet to reach the prey (Eberhard 1990). Theridiidae webs with aerial sheets are present in some *Anelosimus, Tidarren* and *Achaearanea*, e.g., *A. disparata, A. tesselata*, and *A. japonica* (Darchen 1968; Eberhard 1972; Shinkai & Takano 1984). However, the attack behavior associated with the presence of a sheet in the web is very different between genera and species. Some social species of *Anelosimus* attack prey from below the platform (Levi 1972), similar to some *Tidarren* (pers. obs.), other *Anelosimus* that build sheets with knockdown lines, attack insects entangled either in trap lines or in the sheet (Avilés & Salazar 1999; Vakanas & Krafft 2001). In *Achaearanea*, the spiders of the social species *A. disparata* descend directly from the retreat to the prey on the sheet without passing through this structure to access prey (Darchen 1968; Darchen & Ledoux 1978) contrary to *A. tesselata*; no information is available for *A. japonica*.

The unusual web design probably has likely shaped, at least partially, the evolution of the complex attack behavior of *A. tesselata*. Many *Achaearanea* species construct three-dimensional gum-foot webs, specialized for walking prey and/or working as knock down traps (Gertsch 1949); this type of web is ancestral in Theridiidae (Levi & Levi 1962; Benjamin & Zschokke 2003; Agnarsson 2004). Similarly, the presence of a retreat suspended in the upper mesh is common in species of *Achaearanea*, and is also a feature present in other genera, such as *Tidarren* and *Theridion* (Bristowe 1958; Agnarsson 2003). Falling upside down from the retreat also occurs as an escape response in *Argyrodes* (Whitehouse 1986), *A. lunata* (Clerck 1757) (= *T. lunatum*) (Nielsen 1932), *A. tepidariorum* (C. L. Koch 1841) and in *Tidarren* sp. (G. Barrantes unpubl. data) when spiders are disturbed, suggesting that this behavior is also widespread in theridiids. Therefore, the construction of a sheet in *Achaearanea* seems to be newly evolved. Thus, *A. tesselata*, retaining the theridiid retreat trait, presents a novel behavior that allows her to pass through the sheet and access prey from underneath; this novel behavior probably derived from a former escape behavior.

Some elements of the sequence of the attack behavior were fairly variable such as the descent to approach the prey, while the position of legs and body when the spider passed through the sheet showed very little variation. The speed and movements of this spider when the prey is approached seemed to be determined primarily by the size and type of prey, though position of prey on the sheet and hunger may also determine attack speed (Riechert & Luczak 1982). Highly rewarding harmless prey with high probability of escaping (e.g., houseflies) released the fastest reaction: free fall descent (Table 1). When the prey was a treehopper, the approach was slow. The strong kicks from the hind legs of treehoppers can probably cause serious injuries to spiders. The harmless drosophilids were also approached slowly, possibly as a consequence of the little reward these prey represent to mature females of *A. tesselata*. This indicates that *A. tesselata* is either capable of sensing prey type and how dangerous the prey could be, and of modifying the capture sequence accordingly (Riechert & Luczak 1982); or it may attack faster prey sending strong signals (e.g., high buzzing) as they may have greater reward.

The spiders' consistent positions while passing through the sheet are probably a response to the high density of threads in this structure relative to the size of the spider. The position of the body and legs when striking the sheet offered the least contact area, and the high speed at the moment of impact (even after a slow descent) may help to insert femur-patella joints between two threads and open enough space for the spider to pass through. The absence of perceptible damage caused to the sheet during an attack, reported by Eberhard (1972), is largely determined by the numerous unattached lines that form part of this structure (Table 3). These lines are probably easily separated when spiders strike the sheet. The consistent orientation of the body, positions of the legs, and behavior as the spider passed down through the sheet largely contrasted with the inconsistent uncoordinated movements of the spider going upward through the sheet after an unsuccessful attack. Intense selection on prey capture success may have reduced variation in downward movements to increase the rapidity of attack (Eberhard 2000). An obvious advantage of attacking prey from underneath is to interpose a protective barrier between the spider and the prey.

The tangled mesh of the web of *A. tesselata* transmits precise information on prey location to the spider in her retreat. Spiderlings are also capable of perceiving prey location through information transmitted by mesh lines. This is probably due to the convergence of most mesh lines that connect with the sheet below on five or six more or less horizontal threads attached to the mouth of the retreat where the spider hangs (Jörger & Eberhard pers. comm.). This structure may channel vibrations to the central point where the spider rests. Probably information is yielded by vibrations or changes in tension produced by the prey, as occurs in *Latrodectus* (Lamoral 1968). This information allowed the spider to orient her attack before initiating her descent. In contrast, information of prey position was not efficiently transmitted to the spider when prey fell and entangled on mesh lines, as the spider's orientation was imprecise. The reason for this imprecision, in terms of thread connection, is not clear. Thus the design of the mesh in *A. tesselata* may increase efficiency of capture success of prey trapped on the sheet.

The diversity on web designs and frequent convergences in the Theridiidae (Benjamin & Zschokke 2003; Agnarsson 2004) offer an opportunity to study the interrelation of web design and attack behavior. For example a comparative study of *Achaearanea* species with similar web design, could provide a better understanding of the evolution of the attack behavior in the genus, and the function of the upper mesh in transmitting information on prey location.

ACKNOWLEDGMENTS

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MOLECULAR PHYLOGENETIC EVIDENCE FOR THE PARALLEL EVOLUTION OF ROCK ECOMORPHS IN THE NEW ZEALAND ORB-WEAVING SPIDER *WAITKERA WAITAKERENSIS* (FAMILY ULOBORIDAE)

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ABSTRACT. The genus *Waitkera* is the only New Zealand representative of the family Uloboridae and is known from a single species, *Waitkera waitakerensis*. This species is found in forests of the North Island, where it constructs orb-webs on understory vegetation. Rock outcrops in the Northland region support populations of *W. waitkerensis* comprised of larger individuals than those found elsewhere on the island, including those in surrounding forests. Parsimony analyses of DNA sequences from the mitochondrial NADH dehydrogenase subunit ND1, using *Siratoba refernes*, another basal uloborid, as an outgroup, did not delineate these rock-dwelling populations as a monophyletic lineage that could be regarded as a distinct species. A TCS analysis leads to the same conclusion, suggesting that rock-dwelling populations represent independently evolved ecotypes. Northland populations of *W. waitakerensis* are phylogenetically basal; indicating that the species' range contracted northward during the Pleistocene and recolonized the remainder of the North Island.

Keywords: Araneae, Uloboridae, phylogeography, ND1 mitochondrial DNA, nested clade analysis

The monotypic genus *Waitkera* (Opell 1979) is New Zealand's only representative of the family Uloboridae. *Waitkera waitakerensis* (Chamberlain 1946) is comprised of small spiders (Fig. 1) that construct horizontal orb-webs in understory vegetation (Fig. 2). Females have a cephalothorax-abdomen length of 4–5 mm and males of 3–4 mm. Adult female mass averages 9 mg (Opell 1999). Evidence of this species can also be found in their peaked, triangular egg sacs (Fig. 3) that are deposited at the edges of their webs. In the Northland region, egg sacs are first produced in early to mid January and spiderlings begin to emerge from them about one month later (Opell unpublished observations). There are few published records of *W. waitakerensis* (Forster 1967; Forster & Forster 1999). However, this species is sometimes the most numerous orb-weaver in a forest (Opell unpublished observations) and I have collected it from localities throughout the North Island (Fig. 4) in kauri-podocarp-hardwood, lowland podocarp-hardwood, and lowland hardwood forests. I did not observe *W. waitakerensis* in beech forests of the Huiarau or Ruahine Ranges, the extent of my searches in this habitat.

Pleistocene glaciation affected populations of New Zealand's terrestrial arthropods (Trewick 2001) and is likely to have impacted *W. waitakerensis*. The restriction of this species to New Zealand's North Island suggests that during the Pleistocene (New Zealand Wanganui series) this, and perhaps other species of the genus, may have been eliminated from the South Island. In fact, during the Pleistocene, it is probable that the range of *W. waitakerensis* contracted to the warm climate forests that persisted only in the Northland region (Suggate 1978; Thornton 1985). Other events may have contributed to the extirpation of these spiders. The eruption of the North Island's Taupo Volcano 20,000 years ago (Thornton 1985) and again about 1855 years ago (Wilson & Walker 1985) formed deep ash fields that extended for hundreds of kilometers (Fig. 4). These eruptions have impacted populations of other species (McDowall 1996; Morgan-Richards et al. 2000, 2001) and would have been catastrophic for orb-weaving spiders living in the central portion of the North Island.

It is possible that additional species of *Waitkera* survived these events by occupying refugia (Pielou 1991; Pfenninger et al. 2003; Trewick 2001). A likely place for these refu-
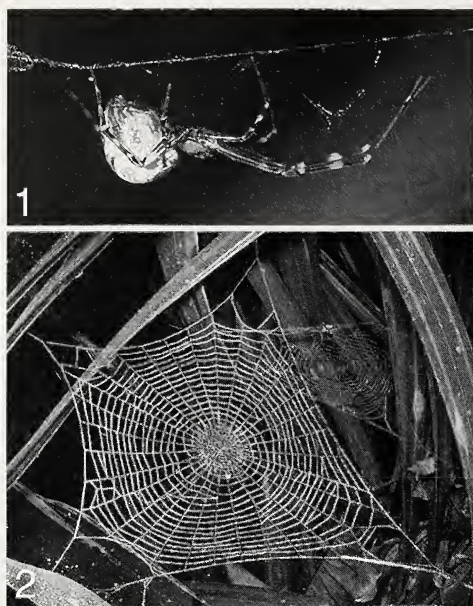
Figures 1–2.—*Waitkera waitakerensis*: 1. Adult female on web; 2. Horizontal orb-webs.

Figure 3.—Egg sacs of *W. waitakerensis* attached at the edge of an orb-web.

gia is the Northland region, which has been collected less thoroughly than most regions of New Zealand and in which cryptic species have been discovered (Gleeson et al. 1999). In this region I discovered a population of *Waitkera* that appeared to represent such a relict species. These spiders were living in the cool, shaded rock crevices of the Waro Limestone Reserve, near Hikurangi (Fig. 5, population 4; Hawley 1981). These crevices extended deep into this karstic area, as evidenced by the cool air coming from many of them. At this site, the spiders, their webs, and their egg sacs were conspicuously larger than those of forest-dwelling populations elsewhere on the North Island, including those in the vicinity of this reserve.

The Waro rock formation is the textbook example of an extensive formation of soft Oligocene limestone that, after being uplifted by the collision the Indo-Australian and Pacific plates, slid westward to form the surface of the eastern one-third of the Northland region (Fig. 5; Suggate 1978; Thornton 1985). I found populations of the larger, rock-dwelling *Waitkera* in outcrops of this formation at three additional sites: Waiomio Glow Worm Cave near Kawakawa, Abbey Caves east of Whangarei, and Waipu Caves south of Whangarei (Fig. 5, populations 19, 6, and 8, respectively).

Figure 4.—Sites at which *W. waitakerensis* was observed by B. Opell. Numbers refer to localities given in Table 1. Heavy dashed lines denote the boundaries of ash deposited by the eruption of the Taupo Volcano about 20,000 years ago and light dashed lines for an eruption about 1855 years ago (Thornton 1985; Wilson & Walker 1985).
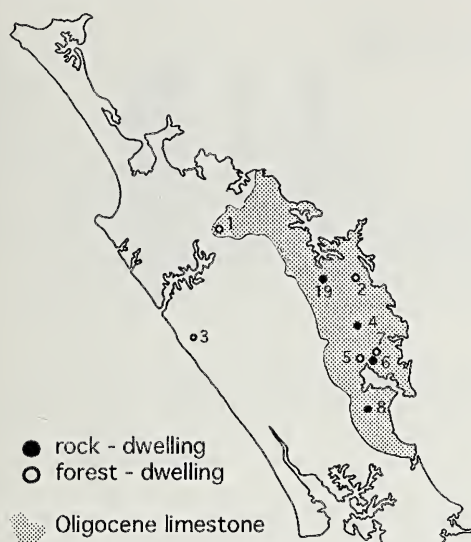
Figure 5.—Oligocene limestone distribution in the Northland and localities of rock-dwelling and forest-dwelling populations in this region. Numbers refer to localities given in Table 1.

There, appears to be no mechanism for direct gene flow between these rock-dwelling populations. A distance of about 12 km separates the closest rock-dwelling sites. *W. waitakerensis* does not appear to be troglophilic. I did not find these spiders either at the entrances of Waipoua Cave, Abbey Caves, or Waipu Cave or in the first 20 m of these caves.

Ecological and morphological evidence suggest that the rock-dwelling *Waitkera* populations may represent one or more undescribed species. However, more convincing support for this hypothesis would come from documentation that these populations form a monophyletic lineage. In this case, such evidence can best come from a molecular comparison of these populations. Therefore, I examined the relationships among *Waitkera* populations using DNA sequences of the mitochondrial NADH dehydrogenase subunit ND1. This rapidly evolving gene has been used successfully to reconstruct the phylogenies and examine the population structure of other closely related spider species (Hedin 1997a, 1997b; Hedin & Maddison 2001; Masta & Maddison 2002).

METHODS

Morphology.—To document the morphological differences among populations, I used a Wild M8 dissecting microscope equipped with an ocular reticle to measure the first femur lengths of ten alcohol-preserved adult female specimens from each of nine forest-dwelling populations and four rock-dwelling populations. I compared the mean femur lengths of these fourteen populations using a Ryan-Einot-Gabriel-Welsch Multiple Range Test (alpha = 0.05) (Day & Quinn 1989) performed with the SAS statistical program (Cary, North Carolina) run on a personal computer. *W. waitakerensis* females have a large, spherical median spermatheca (Opell 1979). To examine differences in reproductive morphology relative to somatic features, I measured the carapace lengths and spermathecal widths of 24 forest-dwelling females from localities throughout the North Island and of five females from each of the four rock-dwelling populations. Carapace length was measured under a dissecting microscope. Spermathecal width was measured under a compound microscope from a genital region that had been removed, cleared in clove oil, and temporarily mounted on a microscope slide under a cover slip. Voucher specimens from each of these populations have been deposited in collections of Landcare Research, Auckland and the Otago Museum, Dunedin, New Zealand.

Molecular.—The molecular study included 40 specimens from 18 populations: 3 Northland rock populations, 5 Northland forest populations, 2 populations from the north central region of the island, and 8 populations from the central and southern regions of the island (Table 1; Fig. 4). I used two specimens of *Siratoba referens* (Muma & Gertsch 1964) from the vicinity of Portal, Cochise County, Arizona as an outgroup for *W. waitakerensis*. This was the most basal uloborid (Coddington 1990) for which I could obtain DNA. Voucher specimens from each of these populations have been deposited in the collections of the Otago Museum, Dunedin, New Zealand.

I extracted DNA from these alcohol-preserved specimens using a Puregene DNA isolation kit from Gentra Systems, Inc. and used PCR to amplify the double-stranded ND1 subunit of mitochondrial NADH dehydrogenase, employing the primers and thermocycler parameters described by Hedin (1997a). For each specimen, I obtained the sequences of both DNA strands using cycle sequencing, Biosystems' Big Dye Terminator™ chemistry, and a 3100 genetic analyzer instrumentation from Ap-

Table 1.—Localities and their haplotypes. Locality numbers correspond to sites shown in Figures 4 and 5, the values plotted in Figures 6 and 7, and the distribution of haplotypes depicted in Figure 8. Specimens from localities 19 and 20 were not included in phylogenetic analyses.

Locality numbers	Locality	°Latitude	Longitude	Habitat	Individuals per haplotype
1	Mangamuka Bridge, Omahuta State Forest	-35.2273	173.5880	forest	1 H1
2	Russell State Forest, near Punaruku Road	-35.3799	174.2438	forest	1 H1, 1H2
3	Waipoua Forest	-35.6164	173.5405	forest	1 H1, 1 H7, 1 H8
4	Hikurangi, Waro Limestone Scenic Reserve	-35.5837	174.2864	rocks	3 H1
5	Whangarei, Coronation Scenic Reserve	-35.7303	174.3093	forest	2 H1, 1 H6
6	Whangarei, Abbey Caves Reserve	-35.7112	174.3574	rocks	3 H1
7	Whangarei, Reed Memorial Kauri Reserve	-35.7071	174.3207	forest	1 H4
8	Waipu Caves	-35.9396	174.3463	rocks	2 H1, 1 H3, 1 H9
9	Karekare, McReady Paddock	-36.9904	174.4675	rocks	1 H9, 1 H16
10	Manaia, Mahakirau Reserve	-36.8551	175.6121	forest	1 H10, 1 H11
11	Mapiu, Aratoro Scenic Reserve	-38.3295	175.1712	forest	2 H12
12	Te Whaiti	-38.5873	176.7816	forest	2 H9
13	Anaura Bay, walkway	-38.2378	178.3298	forest	2 H12
14	New Plymouth, Meeting of the Waters Scenic Reserve	-39.1416	174.1487	forest	1 H12, 1 H15
15	Owhango, Ohinetonga Scenic Reserve	-38.9916	175.3673	forest	2 H14
16	Urewera National Park, L., Waikaremoana, Lou's Lookout	-38.7373	177.1030	rocks	1 H12, 1 H13
17	Dannevirke, Ngapaeruru Scenic Reserve	-40.2616	176.2328	forest	2 H12
18	Paekakariki, Kapiti Borough Council Reserve Walkway	-40.9844	174.9441	forest	2 H12
19	Waiomio Glow Worm Cave near Kawakawa	-35.4144	174.0646	rock	2 H12
20	Hamilton	-37.7815	175.2817	forest	
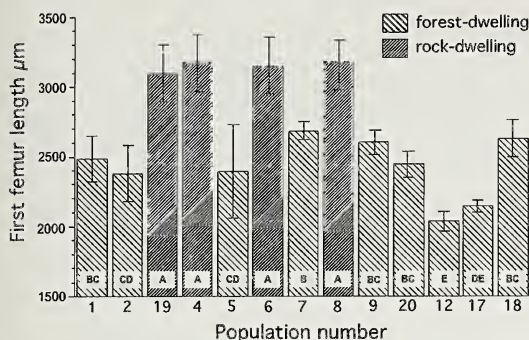
Figure 6.—Histogram of adult female first femur lengths of rock-dwelling and forest-dwelling populations, arranged (from left to right) in a north to south order. Population numbers refer to localities shown in Figures 4 and 5 and described in Table 1. The sample size for each population is 10 individuals. Error bars denote ± 1 standard deviation. Letters within histogram bars denote the ranking of mean values assigned by a Ryan-Einot-Gabriel-Welsch Multiple Range Test (alpha = 0.05) (Day & Quinn 1989).

Figure 7.—Plot of adult female *W. waitakerensis* spermatheca width and carapace length. Population numbers refer to localities shown in Figures 4 and 5 and described in Table 1.

plied Biosystems. Each electropherogram was edited with the EditView program and then aligned with its complementary sequence. Discrepancies were reedited and new sequencing reactions were run when required. Clustal V (Higgins et al. 1996), as implemented by DNA Star, was used to align sequences.

Maximum parsimony and maximum likelihood analyses were implemented with Paup* 4.0b10 (Swofford 1998). Modeltest 3.6 (Posada & Crandall 1998) was run using the likelihood scores generated by PAUP under the "longfmt=yes" option of the Lscores command to determine the preferred maximum likelihood model. The selected model and its values were entered into the maximum likelihood settings of PAUP. The TCS program (Clement et al. 2000) was used to perform Templeton, Crandall, Sing analysis (statistical parsimony analysis; Crandall et al. 1994; Templeton 1998; Templeton et al. 1992). The GeoDis 2.2 program (1999–2004 David Posada) and its June 2004 inference key (Templeton et al. 1995; Posada & Templeton 2000) were used to perform a nested haplotype analysis (Templeton et al. 1987; Crandall 1994, 1996).

RESULTS

Morphology.—Spiders from the four rock-dwelling populations were larger than those from the ten forest-dwelling populations (Fig.

6). These size differences are also reflected in male and female genitalia, although there are no qualitative shape differences, perhaps due to the very simple nature of the genitalia (Opell 1979). As Figure 7 illustrates, rock-dwelling females have larger spermathecae than forest-dwellers. This may simply be a reflection of the larger body size of rock-dwellers, although recent molecular studies of millipedes and spiders show that genitalic morphology can underestimate species diversity (e.g., Bond & Sierwald 2002; Bond et al. 2001). It is interesting to note that spermathecae of three of the four rock-dwelling populations are as distinct from one another as they are from the forest-dwelling populations. This could suggest that even greater diversity is represented among the rock-dwellers or that these populations exhibit more phenotypic plasticity than do forest-dwelling populations.

Molecular analysis.—After uncertain terminal DNA regions were eliminated, 412 base pairs were available for analysis. Three insertions in each *W. waitakerensis* sequence were necessary to align the DNA of this species with that of *S. refernes*. No additional insertions or deletions were necessary. Sequences of both *S. refernes* specimens were identical. Sixteen DNA haplotypes with a mean uncorrected (p) distance of 0.94% (range 0.24–1.71%) were represented by the 40 *W. waitakerensis* specimens (Table 1). The distance between *W. waitakerensis* haplotypes and *S.*
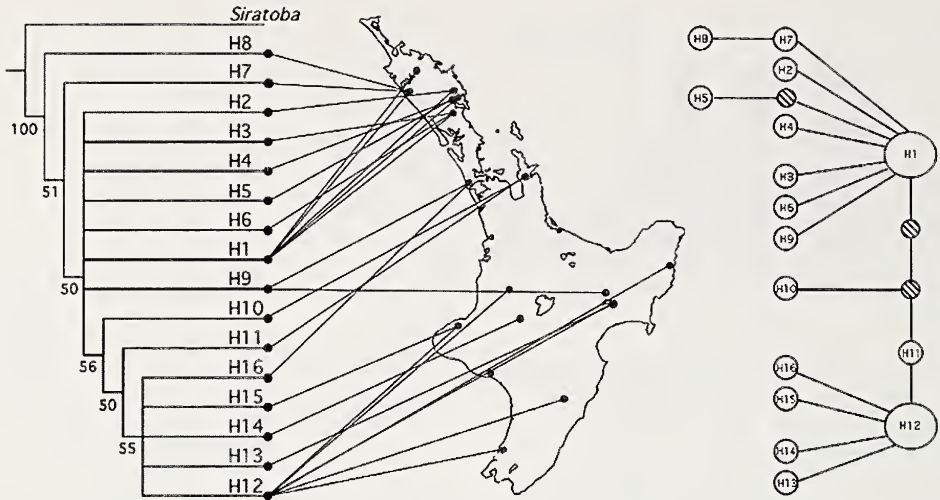
Figure 8.—Parsimony analysis of 16 *W. waitakerensis* ND1 haplotypes run with *S. referens* as an outgroup and mapped onto localities (left) and statistical parsimony (TCS) network of these haplotypes (right). Parsimony analysis is the single tree from a branch and bound search, CI = 0.9846, RI = 0.9231, number of informative characters = 116 (6 within *W. waitakerensis*), 50% majority-rule consensus bootstrap values from a 2000-replicate analysis. In the TCS network open circles represent the haplotypes and cross-hatched circles inferred missing haplotypes. Each line connecting a haplotype represents a single change in one base pair.

referens was 27.6–28.3%. GenBank accession numbers: Siratoba = DQ026788, H1 = AY974175, H2 = AY974176, H3 = AY974177, H4 = AY974178, H5 = AY974179, H6 = AY974180, H7 = AY974181, H8 = AY974182, H9 = AY974183, H10 = AY974184, H11 = AY974185, H12 = AY974186, H13 = AY974187, H14 = AY974188, H15 = AY974189, H16 = AY974190.

Maximum parsimony analysis (branch and bound search) produced a single tree (Fig. 8). Modeltest selected a HKY model and provided the following values used in PAUP's likelihood settings: Ti/tv ratio = 2.6311, empirical base frequencies, among-site rate variation = 0, variable sites = equal rates for all sites, maximum number of branch-length smoothing passes = 20, parameterization for clock model = standard, starting branch lengths for non-clock models = least squares method, Jukes-Cantor. A heuristic search produced a single tree (-Ln likelihood = 994.95) that was identical to that shown in Figure 8. An attempted branch and bound search was terminated after four days of computing.

Parsimony analysis (Fig. 8) roots the tree at two haplotypes (H7 & H8) from Waipoua Forest (locality 3) in the west of the Northland.

Relationships among the remaining Northland haplotypes (H1–6 & H9) are not resolved, providing no support for the hypothesis that rock-dwelling populations constitute a distinct lineage. Furthermore, individuals from the three included rocky sites share haplotype H1 with individuals from Northland forest sites. Two Coromandel Peninsula haplotypes (H10–11) lie at the base of a clade that is sister to the unresolved northland haplotypes and terminates in five unresolved central and southern haplotypes (H12–16). The only two haplotypes not explained by a strict cladogram base-to-tip = north-to-south pattern are H9 and H16. H9 is represented both at locality 9, which is consistent with the general pattern, but also at locality 12, a more southern site. H16 is represented at locality 9, a more northern locality than those occupied by the four other members of its unresolved, otherwise southern clade.

Siratoba referens is too distantly related to *W. waitakerensis* to be included in the 95% confidence limits of the statistical parsimony network (Fig. 8). However, if this network is rooted at haplotype H8, its pattern is identical to that of the parsimony analysis. A nested haplotype analysis of geographical distances based on this network (Fig. 9) and distribution
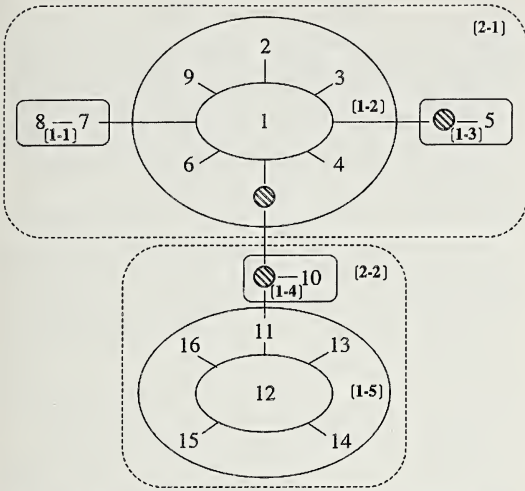
Figure 9.—Haplotype network arranged in hierarchical format for nested haplotype analysis of geographical distances. Numbers within brackets identify the nested clades. Other numbers identify the haplotypes, shown in Fig. 8 and Table 1.

data given in Table 1 was inconclusive. It was unable to determine if the current distribution of *W. waitakerensis* is explained by past fragmentation of a more inclusive distribution, by continuous range expansion, by long distance dispersal, or by combinations of these events. Exact contingency tests for all subclades were insignificant ($X^2 > 7.98$, $P > 0.16$). The exact contingency test for the total cladogram was significant ($X^2 = 37.95$, $P < 0.001$). For this clade (comprised of subclades 2–1 and 2–2) the inference key led through the following couplets: 1, 19, 20 (here, I considered sampling adequate to answer "yes"; however, an answer of "no" leads to the conclusion "inadequate geographic sampling"), and 2, where the conclusion is "tip/interior status can not be determined—inconclusive outcome". This GeoDis analysis placed the geographic center of clade 2–1 in the Northland, just north of Whangarei (between sites 4, 5, and 7) and the geographic center of clade 2–2 northwest of Lake Taupo (just east of site 11).

DISCUSSION

Phylogenetic analyses offer no support for the hypothesis that the rock-dwelling populations of large-bodied *W. waitakerensis* represent a monophyletic lineage that might be considered a species. Some of the individuals from each of these populations share a hap-

lotype with individuals from forest populations. Two unique haplotypes were included in one of the rock-dwelling populations, but these were no more divergent than other unique haplotypes found among Northland forest-dwellers. Thus, rock-dwelling populations appear to represent an ecotype that has arisen multiple times. These populations of *W. waitakerensis* may represent lineages that have recently adapted to karstic areas and have had insufficient time to diverge genetically. As such, they may represent a group of incipient or cryptic species. ND1 DNA may not have diverged rapidly enough to serve as an appropriate genetic marker and other genes might better delineate individuals from rock-dwelling populations. Adult rock-dwelling and forest-dwelling populations do not appear to be temporally isolated, although their microhabitats tend to isolate them physically. Genitalic size differences may also limit gene flow between rock and forest populations, but the simple genitalia of *W. waitakerensis* (females are functionally haplogyne; Opell 1979) may minimize the difficulty of mating by individuals of dissimilar sizes.

The larger size of rock-dwelling spiders in the Northland does not initially appear to conform to intraspecific size clines that characterize many terrestrial arthropods with univoltine life cycle. Larger individuals are typically found in warmer regions at the lower latitudes or lower elevations of a species' range (e.g., Masaki 1978; Mousseau & Roff 1989; Orr 1996; Schoener & Janzen 1968; Scott & Dingle 1990). These warmer regions have longer growing seasons that permit individuals to attain larger adult sizes (Mousseau 1997), a pattern that appears to have an underlying genetic component (Huey et al. 2000). These observations suggest that it may be more appropriate to consider rock-dwelling populations of *W. waitakerensis* as living in more thermally stable microhabitats rather than simply in cooler microhabitats. Under this scenario, spiders in karstic microhabitats would be protected from the low and fluctuating spring temperatures experienced by forest-dwellers and, consequently, would have a longer developmental period permitting them to attain a larger adult size than forest-dwellers.

The population structure of *W. waitakerensis* (Fig. 8) is consistent with a contraction of the species' range to the Northland region

during the Pleistocene glaciation. The most basal haplotypes (H7 & H8) are found in the Northland, as are seven haplotypes derived from them. As the climate warmed, this species recolonized the North Island by way of the Coromandel Peninsula (haplotypes H10–11). Access to more direct central and western corridors may have been blocked by extensive volcanic activity in the Auckland area (Suggate 1978; Thornton 1985). However, this corridor later opened, allowing southern migration of haplotype H9 and northern migration of haplotype H16 into the species' type locality in the Waitakere Mountains north of Auckland (locality 9). This species may have ballooned to the Coromandel Peninsula or it may have expanded southward along with warm climate coastal forests. Colonization of the North Island's central and southern regions appears to have been rapid and perhaps recent, given the occurrence of a common haplotype (H12) at six widely separated sites. The spread of *W. waitakerensis* below the 38th parallel may have been halted or set back by the most recent eruption of the Taupo Volcano (Fig. 4; Wilson & Walker 1985) and populations in the southern half of the North Island may be of very recent origin.

The phylogenetic pattern of *W. waitakerensis* may be characteristic of other New Zealand spiders that require a mild climate and have limited dispersal capabilities. If so, this study indicates that the Northland and Coromandel Peninsula regions, though small in area, contain critical elements of New Zealand's biodiversity.

ACKNOWLEDGMENTS

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SHORT COMMUNICATION

OBSERVATIONS ON COURTSHIP AND COPULATION OF THE WOLF SPIDER *RABIDOSA SANTRITA* (ARANEAE, LYCOSIDAE)

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ABSTRACT. In this note, I describe courtship and mating behavior of the wolf spider *Rabidosa santrita* (Chamberlin & Ivie 1942) from riparian habitat in southeastern Arizona. Males responded to substrate-borne cues of females with several distinctive behaviors: they walked slowly, following female web draglines; with their palps, they plucked the dragline and/or tapped on the substrate near the dragline; and they performed raises and extensions of legs I, "tapping" the tips while in midair. On substrate previously occupied by another male, these behaviors were either not done or males performed them more rapidly, and for a shorter duration. Males initiated courtship, which consisted of taps or short strokes of legs I of the female by the male's legs I. Copulation was similar to that described for other species of *Rabidosa*. Males inserted one palp at a time, performed one hematodochal expansion per insertion, moistened the palp following insertion, and alternated palps for each insertion. Copulation lasted from 35 min to >1 h.

Keywords: Courtship behavior, mating behavior, pheromones, substrate-borne cues, dragline, silk

The genus *Rabidosa* Roewer 1960 comprises five species of medium to large sized wolf spiders found primarily in the United States (Brady & McKinley 1994). For this genus, behaviors related to courtship and mating have been described most thoroughly for the widespread species *R. rabida* (Walckenaer 1837). Female *R. rabida* produce pheromone-laden silk draglines, which males use to locate females (Tietjen & Rovner 1982). Once an encounter has occurred, a male may use both visual and auditory signals during courtship (Rovner 1968, 1975). A male that courts successfully mounts the female so they face in opposite directions, inserts a palp into one side of the female's epigynum, and expands the hematodocha once to force sperm into the female's copulatory tubes. As the male shifts to the opposite side, the female responds by rotating her abdomen, enabling the male to insert his other palp in the opposite side of the epigynum (Rovner 1968, 1971). Males repeat this process a number of times and copulation can last for over an hour (Rovner 1972; Stratton et al. 1996).

Courtship and mating behaviors are poorly known for the remaining *Rabidosa* species. As for *R. rabida*, male *R. punctulata* (Hentz 1844) locate females by following their draglines (Tietjen & Rovner 1982). Copulatory behavior in *R. punctulata* and *R. hentzi* (Banks 1904) also resembles that of *R. rabida*, as males assume the same orientation to the female and perform one insertion and he-matodochal expansion before switching to the opposite side of the epigynum (Stratton et al. 1996). No description of courtship or mating behaviors exists for the other two species, *R. carrana* (Bryant 1934) and *R. santrita* (Chamberlin & Ivie 1942).

Rabidosa santrita is the only member of the genus found in the western United States and is considered the sister species of *R. rabida* (Brady & McKinley 1994). Kronk & Riechert (1979) have shown that both sexes of *R. santrita* prefer woodland (grassy) areas as juveniles but move closer to streams as adults, and Stratton et al. (2004) have examined locomotion of this species on the water's surface. However, little else is known of this species. In this note, I characterize behaviors exhibited by male *R. santrita* in the presence of chemical cues from male or female conspecifics. I next outline courtship and copulatory behaviors observed in a series of laboratory trials and compare the results to observations of other *Rabidosa*.

I collected 26 *R. santrita* (15 males, 11 females) on 17 June 2004 from the cobble zone along Cave Creek on the grounds of the American Museum of Natural History's Southwestern Research Station, located in the Chiricahua Mountains southwest of Portal, Cochise Co., Arizona (31.9147°N, 109.14795°W). Spiders were collected at night while active on the cobble surface, and all were in the penultimate or antepenultimate instar when captured. Spiders were housed individually in 0.95 l

translucent containers fitted with a perforated lid. Each container had a substrate of moistened peat moss ~1 cm deep and a crumpled piece of paper towel to serve as a refuge. I offered spiders 2–3 juvenile crickets weekly. The laboratory was kept on a 13L:11D photoperiod and at a temperature of 21–24 °C. Voucher specimens have been deposited at the Denver Museum of Nature and Science.

By mid-September, all spiders had undergone their final molt. Between 7–28 October, I performed a series of trials to examine male behaviors on substrate previously occupied by either an adult male or adult female conspecific to determine if males could detect and differentiate between chemical cues left by either sex. I used 15 males for these trials, testing each on both male- and female-occupied substrates. I randomized the order of substrate presentation across males.

Test chambers were 10 × 10 × 8.5 cm transparent plastic containers with a layer of moistened peat moss ~2 cm deep and fitted with a perforated lid. I placed a single adult male or female (the "cue" spider) into each chamber and kept it there for 4 days, during which time all spiders deposited silk and (presumably) excreta. Prey were not available to the cue spiders in the test chamber; however, each had been offered crickets 24 h before introduction to the test chamber. A total of eight cue females (1–3 trials per spider) and 10 cue males (1–2 trials per spider) were used.

To begin a trial, I removed the cue spider and then introduced a single male "trial" spider into the center of a test chamber. Each trial spider had been fed the same day as the cue spider, and had been held in a large centrifuge tube for 15–30 min before being placed in the test chamber. I then observed each trial spider for 1 h. All trials were conducted between 1000 and 1330 h. Following a trial, I thoroughly cleaned test chambers and lids with warm water, swabbed all surfaces with ethanol, and allowed them to air dry before re-use with another cue spider.

Male behaviors on substrate previously occupied by a female differed from those on substrate previously occupied by another male. In the following, I provide general qualitative descriptions of male behaviors on substrates with each type of cue; however, individual males differed somewhat in the order in which behaviors were performed, and not every male performed each of the behaviors described for a particular substrate.

On substrate previously occupied by a female, males usually remained stationary for several minutes after introduction to the test chamber. Once active, males performed several distinctive behaviors on encountering female cues (most often draglines). First, males were seldom completely immobile and, when walking, moved at a slow pace;

running or normal-paced locomotion was not observed after contact with female cues.

Second, males performed several actions with their palps. One action involved pulling, or plucking, on the dragline, and males typically alternated palps while performing this behavior. This may be a form of trail following behavior, as described for *R. punctulata* and *R. rabida* (Tietjen & Rovner 1982). Males also tapped the substrate on or near the dragline, again with an alternation between palps. This appears to be chemoexploratory behavior, again similar to behaviors observed in *R. punctulata* and *R. rabida* (Tietjen & Rovner 1982). Finally, males occasionally touched their ventral body surface with one palp or with both palps simultaneously.

A third action observed on female-occupied substrate involved raising and extension of legs I. This behavior began when a stationary or slowly moving male raised a single leg I (or, less frequently, both first legs) to an angle of ~45–80° with the substrate. When fully raised, the leg was held straight; this position could be maintained for up to a minute, although the duration was typically <10 s. The leg was then brought down toward the ground while fully extended forward. Shortly after this downward motion began, males typically jerked or "tapped" the metatarsus and tarsus several times (what I have called an "air tap"). Males generally performed this behavioral sequence multiple times within a bout, either by alternating legs I or, less commonly, by repeatedly using the same leg. Rarely, males raised and extended a leg II, either alone or in conjunction with leg I. However, air taps were never performed by leg II. This overall sequence in *R. santrita* differed from leg I extensions of *R. rabida* in several ways (Rovner 1968), notably the way the leg was held when raised (in *R. rabida* it is held in a flexed position) and the presence of air tapping (which is absent in *R. rabida*).

Males placed in contact with conspecific male cues were generally immobile for a large portion of the observation period, often while remaining stationary on the cue male's silk. However, when active, males moved more rapidly than when in the presence of female cues. Many of the trial males tapped and/or plucked at cue male draglines with their palps and performed leg I raises and extensions, but these always differed from similar behaviors done in the presence of female cues. Males performed both palpal plucking/tapping and leg I raises more rapidly and for a shorter duration on male-occupied substrate. I never observed air tapping in this context.

Overall, 14 of 15 males performed each distinctive courtship behavior (slow movement; slower palpal plucking and tapping; multiple leg I raises and extensions with air taps) in the presence of female cues, while none of the males performed these

behaviors in the presence of male cues. The male that did not respond to female cues climbed into a corner of the test chamber and remained motionless for the entire observation period.

In a second set of trials, I examined courtship and mating behaviors of *R. santrita*, using six pairs of virgin spiders (although each male had prior exposure to female cues during chemosensory trials). I conducted trials on 2–3 December 2004, between 0930 and 1300 h. For these trials, I used 30 × 17 × 10 cm test chambers fitted with a non-perforated lid and with ~2 cm of moistened peat moss as a substrate. A female, which had been offered 2–3 crickets the previous day, was introduced into a chamber and allowed to deposit silk and excreta for 24 h. I then removed the lid, added a male to the half of the test chamber not occupied by the female, and observed the pair for 1 h. As with the chemosensory trials, males were held in centrifuge tubes for 15–30 min before introduction to the test chamber. Spiders still engaged in copulation at the end of 1 h were allowed to continue mating for up to an additional 1 h but no observations were made during this period.

In all trials, males encountered female draglines, with five of the six males orienting in the female's general direction on first movement. All males performed behaviors identical to those seen in the female-cue chemosensory trials. In particular, males slowly followed a dragline, tapped and/or plucked it with their palps, and performed leg I raises and extensions with air taps. Females appeared able to detect the male's approach at a distance of 5–10 cm. Most females (four of six) simply turned towards the male; however, one female moved forward 2–3 cm as the male approached, and another retreated ~5 cm. In two cases, the male performed palpal taps at a faster rate as he neared the female.

Two distinct behavioral sequences occurred as a male neared a female. In three trials, the female assumed a posture in which she raised her body well off the substrate and lifted her legs I (and, in the case of one female, legs II) straight upward. This posture occurred when the male was ~2–5 cm away, and the female remained in this position until contacted by the male. On contact with the male's leg I, the female lunged at the male, who rapidly retreated; the female then remained in this raised-body posture for several minutes. This sequence (male approach followed by female raised-body posture and lunge) was repeated 2–3 times in each trial, but no female appeared to bite a male. It seems likely that the female's behavior represents an aggressive response to the male, since no copulations occurred in these three trials and the raised-body posture was not performed by females who did copulate.

In the other three trials, the male successfully copulated with the female. Courtship was always initiated when the male's extended leg I touched the female's leg I. This contrasts with the initiation sequence in *R. rabida*, in which the female always made first contact (Rovner 1972). The male repeatedly touched the female's leg(s) I with his leg(s) I for 1–2 min. During this period the female lowered her entire body close to the substrate and extended legs I and II in front of her along the ground. Rovner (1972) describes a similar lowering of the cephalothorax in *R. rabida*. The male then climbed onto the female in the standard lycosid position (Type 3; Foelix 1996), facing her abdomen, and began palpal insertions. Two short video clips of one copulation sequence are available online at "iweb.tntech.edu/cabrown/Rabidosa1.wmv" and "iweb.tntech.edu/cabrown/Rabidosa2.wmv" (or contact the author).

Copulation in *R. santrita* followed the typical pattern found in *Rabidosa* (Stratton et al. 1996). The male inserted one palp at a time, the left into the left epigynal opening and the right into the right epigynal opening. After insertion, the palpal hematodocha expanded a single time. During the time the palp was engaged with the epigynum, the male vibrated his abdomen up and down at a moderate rate. After removal of the palp from the epigynum, the male pulled it several times between his chelicerae, an action termed palpal moistening by Rovner (1972). Palpal moistening was only rarely skipped. The male then shifted to the other side, triggering rotation of the female's abdomen, and inserted the opposite palp into the epigynum. This pattern of insertion and hematodochal expansion by alternating palps continued for 35 min in one pair, and for >1 h in the other two pairs. These times are similar to those reported for *R. hentzi* and *R. rabida* (Rovner 1972; Stratton et al. 1996). For the pair in which I observed the end of copulation, the male dismounted from the female and walked rapidly away, while the female remained motionless for ~5 min. These two spiders then re-encountered one another ~15 min after the end of copulation, resulting in the female assuming a raised-body posture and lunging at the male. Cannibalism of the male occurred in one of the other trials. Since I did not observe the end of copulation or the attack on the male, I do not know if cannibalism occurred immediately after mating or upon re-encounter.

All females that mated produced egg sacs, at 7, 24, and 84 d post-copulation. Only the sac laid at 24 d produced spiderlings; the first-laid sac failed when the female died and the last-laid sac was small and dropped by the female. Two of the non-mated females also produced egg sacs, at 92 and 106 d post-trial. Both sacs were small and dropped by the females. These results may in part reflect the age of the spiders when mating trials were conducted (2 months after the final molt), if mating success of either males or females declines with age (e.g., Hu & Morse 2004).

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SHORT COMMUNICATION

VISCID GLOBULES IN WEBS OF THE SPIDER
ACHAEARANEA TESSELATA (ARANEAE: THERIDIIDAE)

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ABSTRACT.   We describe the presence and dimensions of viscid globules in both the sheet and tangle portions of the webs of *Achaearanea tesselata* (Keyserling 1884). We found viscid globules in all sheets and tangles of the webs examined. The globules were very small and water soluble. The globules were present in the sheet of the first web built by a juvenile ($n = 1$), but their density was lower than in webs of mature females ($n = 6$).

Keywords: Spider webs, viscid silk, web construction

The designs of spider webs and many of their properties probably serve to increase prey capture, the web's principal function (Comstock 1948; Eberhard 1990). For instance, viscid threads typically increase the probability of prey capture since they readily adhere to insects or other prey types that contact the viscid globules present on such threads (Craig 1987). Viscid globules are present on lines of webs of at least eight families in the superfamily Araneoidea (Bristowe 1958; Foelix 1996; Agnarsson 2004) and in Pholcidae (Briceño 1985).

The webs of theridiids are typically described as a three-dimensional mesh with or without a retreat, with long, more or less vertical lines connected to substrates nearby (Nielsen 1932). These long lines are the main trapping portion of the web. In webs of some species of the family Theridiidae, e.g., *Latrodectus* spp., *Nesticodes rufipes* (Lucas 1846), *Achaearanea tepidariorum* (C. L. Koch 1841), these long lines are coated with viscid globules near the ends connected to the substrate (Nielsen 1932; Szlep 1965; Lamoral 1968), but in other species, such as *Theridion evexum* Keyserling, 1884 (Barrantes & Weng in press) and *Chrysso intervales* (n. sp.; Gonzaga et al. 2006) the viscid globules are present along nearly the entire length of the capture lines. However, in the web of *Achaearanea tesselata* (Keyserling 1884), which consists of a dense, more or less horizontal sheet and a dense tangle with a retreat above, viscid globules have not been reported (Eberhard 1972; Benjamin & Zschokke 2003). In this note we report the presence of viscid globules in both the sheet and in the upper tangle of *A. tesselata*. We also describe the size and density of viscid globules in the sheet of this spider's

web. Voucher specimens of the spiders were deposited in the Museo de Zoología, Universidad de Costa Rica.

We estimated the density of viscid globules in the sheets of six webs of mature females in the field and in the sheet of the first web constructed by a juvenile, possibly third or fourth instar. Samples from the sheets were collected on slides framed with strips of double-sided adhesive tape (1.5 mm thick × 2.5 mm wide). The slide was carefully placed against the threads of the sheet from below, and the threads were cut once they adhered to the tape. This method allows observation of threads in the sheet with minimum modification of their original arrangement. Similarly, between three to five threads from the upper mesh were collected from each web. Because the upper mesh in these webs has a three-dimensional arrangement, its threads adhered to the slide and were cut one at a time to reduce any further modification. Slides were placed under the light microscope (40 X) and 10–15 segments of threads were randomly chosen from each sheet; each segment being the length of thread within the diameter of the field of view (0.45 mm). We counted the viscid globules in all segments to estimate their density (number of globules/mm) in the sheet, and measured the width and length of 10–12 of them in each sheet using a micrometer (relative humidity when globules were measure was between 40–50%). We searched for viscid globules on the tangle lines and measured them, but did not estimate their density. We tested whether viscid globules were water-soluble by placing drops of water on slides holding globule-containing sheet threads. The water was allowed to evaporate and when
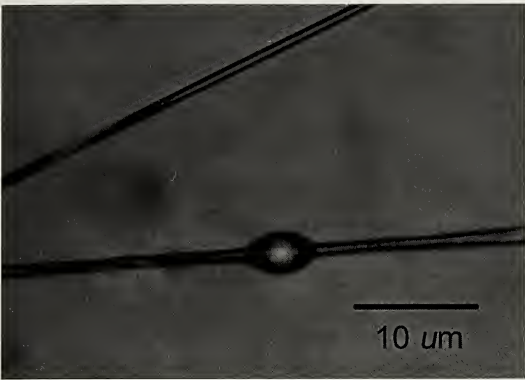
Figure 1.—Viscid globule in a sheet thread of *Achaearanea tesselata*.

threads were again checked the viscid globules had disappeared (Briceño 1985). We also placed some slides with sheet threads, which had been maintained at a relative humidity of about 40%, in a chamber saturated with water vapor. After 2 h, we examined them for any change in size of the viscid globules. These threads were collected during the dry season, following a two-month drought. All samples were collected on the campus of the Universidad de Costa Rica, San José, Costa Rica (9°54′N, 84°03′W; elevation 1200 m).

Viscid globules were present in the sheet (Fig. 1), and the upper tangle of all webs that were examined. The density of viscid globules varied among the sheets examined, and the length of these tiny globules varied more than their width, given a general ellipsoidal shape to the globules (Table 1). The lowest density of viscid globules was in the first web constructed by a juvenile (0.12 globules/mm). In contrast, the highest density (0.62 globules/mm) was observed in a web that had been inhabited for two months by a mature female (time of construction was unknown for the other webs). Otherwise, the web design of the juvenile was indistinguishable from webs of mature females.

The function of the viscid globules in webs of *A. tesselata* is unclear. The tiny size of the viscid glob-

ules suggests that they are of little help in prey retention. However, if viscid globules restrain prey's movements in the sheet, the success of the extremely rapid attack of this spider (Barrantes & Weng unpublished data) would likely increase. Benjamin et al. (2002) proposed that similarly small and sparse globules produced by substance from the aggregate glands in the webs of some linyphiids function as a cementing substance, but this is unlikely given the position of the viscid globules in the web. If the function of the globules is to cement the threads of the sheet they would be expected to be primarily at the intersection or connecting points of the threads. However, the globules in webs of *A. tesselata* (Fig. 1) and most globules in webs of some lyniphiids (Benjamin et al. 2002) were not found at the intersection of threads. Furthermore, the viscid globules in *A. tesselata* were water-soluble as were viscid globules of other groups of spiders (Briceño 1985; Townley et al. 1991); such a condition is not expected for substances that cement the threads of the sheet and tangle of this spider.

Viscid globules in threads from the sheet of *A. tesselata* that were maintained for more than 2 h at a relative humidity of about 40%, increased as much as two times in size after being placed in a humid chamber (ca. 40 min), suggesting the presence of hygroscopic organic compounds, similar to the viscid globules of some orb spiders (Vollrath et al. 1990; Townley et al. 1991). Measuring the stickiness of the globules (Opell 1989, 2002) as well as detailed studies of prey capture in webs at different stages of construction, and in webs that have been washed with water might help to elucidate the function of the viscid globules in *A. tesselata*.

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Table 1.—Overall mean length and width (μm) of viscid globules in the sheet and tangle of webs of *Achaearanea tesselata*; 10–12 droplets were measured to calculate the mean per sheet, and means of the seven sheets were combined to calculate the overall mean. Values in parentheses correspond to the juvenile web (these values were included to calculate overall means). Density (number of globules/mm) of viscid globules is also presented for sheet lines.

	Sheet ($n = 7$)			Tangle ($n = 5$)	
	Length	Width	Density	Length	Width
Mean	9.2 (7.0)	5.2 (5.1)	0.49 (0.12)	9.8	4.6
SD	5.4 (3.8)	2.3 (1.7)	0.20 (0.15)	4.8	0.8
Range	6.3–15.5	5.2–2.3	0.12–1.1	5.0–18.0	4.0–5.3

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SHORT COMMUNICATION

THE FIRST RECORDS OF *MYRMARACHNE FORMICARIA* (ARANEAE, SALTICIDAE) IN THE AMERICAS

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ABSTRACT. A population of *Myrmarachne formicaria* has been discovered in northeastern Ohio. There is reason to believe that this species, which is widespread in Europe, is a recent accidental introduction to this area. This species seems to be well established, having been found with increasing frequency over the past three years. The species appears to be common in a variety of situations, including occasionally inside buildings.

Keywords: *Myrmarachne*, ant-like, introduced species, Ohio

There have been several recent reports of spiders accidentally introduced that have established local populations in North America. These include *Linyphia triangularis* (Clerck 1757) (Jennings et al. 2002); *Synageles venator* (Lucas 1836) (Hutchinson & Limoges 1998); and *Zoropsis spinimana* (Dufour 1820) (Griswold & Ubick 2001). We have discovered yet another such species, *Myrmarachne formicaria* (De Geer 1778). This find represents the first observation of a member of this genus in North America. The large genus *Myrmarachne* (Araneae, Salticidae) includes over 200 species, with representatives on every biogeographic region except the Nearctic.

The first specimen records of *M. formicaria* from North America have all been from Ohio, USA: from Warren, Trumble County on 16 August 2001; the J.H. Barrow Field Station, Portage County on 15 September 2002; and at a residence near Peninsula, Summit County. Additional individuals have been observed by the third author in and around the J.H. Barrow Field Station and the Peninsula residence during the summers of 2003 and 2004. The species appears to be fairly common and is active during the warm months of the year in open areas as well as in buildings. It is sometimes associated with the local ants of the genus *Formica*. It is the only ant-like North American jumping spider in which the male chelicerae project forward more than 50% of the carapace length, and in which the female palpal tarsus is dorsoventrally flattened and bent downward distally.

The date and origin of this presumed introduction are unknown. It seems likely that this species is a recent introduction because it is a relatively large (body length ~ 6 mm), conspicuous and distinctive species, it is hard to imagine that it could have been previously missed. The fact that this spider is day active and prefers open sunny environments, combined with its active foraging behavior make it unlikely that the species would have been overlooked for an extended period. According to Locket & Millidge (1951) "It is a long slender spider with a superficial resemblance to the ant *Formica rufa* Linn. It does not jump, but runs about in the grass, etc., sometimes in company with ants. It is adult in May–July, and is recognisable at once in the field." Other species in the genus *Myrmarachne* are said to associate with particular species of ants (Edmunds 1978). *Myrmarachne formicaria* does appear somewhat similar to one other ant-like salticid that can be found in Ohio, *Sarinda hentzi* (Banks 1913). A search through extant historical collections of *S. hentzi* from Ohio has not yielded additional specimens of *M. formicaria*. It is true, however, that relatively few spider researchers have investigated this portion of Ohio until recently.

Myrmarachne formicaria is a Palearctic species (Platnick 2004). It is tempting to speculate that this species was inadvertently introduced into Ohio from Eurasia via human activities. This is the second species of Eurasian ant-like salticid to be

established in North America in recent years. *Synageles venator* (Lucas 1836) was first noted in the Montreal area in the early 1990's and is now a common house spider in southeast Quebec (Hutchinson & Limoges 1998; Paquin & Dupérré 2003). Possibly *M. formicaria* was imported with planting materials or horticultural plants. The species seems to be well established in Ohio. Individuals have now been observed in four successive years. The fact that the species now occupies a span of over 60 km in localities from three counties in NE Ohio suggests that the species may be expanding its range.

Material Examined.—USA: *Ohio*: Portage County: J.H. Barrow Field Station (41°18′N, 81°08′W), 15 September 2002, R. Bradley, 1 ♀, 1 ♂ (Ohio Spider Survey #SPM010921); Trumble County: Warren (41°13′N, 80°50′W) in residence, 16 August, 2001, T. Robinson, 1 ♂ (Ohio Spider Survey #SPM008004).

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SHORT COMMUNICATION

THE PREY AND PREDATORS OF *LOXOSCELES INTERMEDIA* MELLO-LEITÃO 1934 (ARANEAE, SICARIIDAE)

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ABSTRACT.   We examined the prey caught in *L. intermedia* webs in one fragment of forest and in the garage of an urban house in Curitiba, Brazil. A total of 693 prey items was recorded in 131 webs. The prey richness was greater in the forest. The results show that *L. intermedia* is a dietary generalist. We found remains of *L. intermedia* in the feces of a frog and a bat in the forest.

Keywords: Diet, brown spider, synanthropic fauna, loxoscelism, Brazil, frog, bat

The sedentary species of the genus *Loxosceles* are hunting and weaving spiders active mostly at night. The webs of some species in this genus are durable, large, irregular and sticky, with the spiders constantly adding silk threads to the web, which serves as a retreat and a snare. The webs are built in a great variety of habitats, including around buildings that provide many ideal microhabitats (Bücherl 1961; Hite et al. 1966; Galiano 1967). *Loxosceles* spiders can capture prey in their web or when walking around at night (Gorham 1968). Qualitative lists of the prey captured by *L. laeta* (Nicolet 1932) (Levi & Spielman 1964), *L. rufipes* (Lucas 1834) (Delgado 1966), *L. reclusa* Gertsch & Mulaik 1940 (Hite et al. 1966) and *L. gaucho* Gertsch 1967 (Rinaldi et al. 1997) have been published.

In Curitiba, capital of the southern Brazilian state of Paraná, hundreds of bites caused by *Loxosceles* species are registered each year. Two species occur in the city: *L. intermedia* Mello-Leitão 1934 (with 90% of records) and *L. laeta* with 10% (Fischer 1994). Among the conditions favoring the growth of *Loxosceles* populations in and around urban centers are the abundance and richness of prey and the absence of potential predators. In this study, we documented the range of prey captured in *L. intermedia* webs and recorded the fauna present in the

same microhabitat in one fragment of forest and in a house in Curitiba.

We made weekly visits from December 1993 to March 1995 to a forest located in the Santa Monica field club, in the district of Colombo (25°23′22.9″S, 49°09′01.3″W). The area is up to 950 meters above sea level and the climate is humid subtropical mesothermic, with fresh summers and with severe and frequent frosts (Maack 1981). The native vegetation was transitional between forest with *Araucaria* and Atlantic forest, now replaced in some areas with *Eucalyptus*. The present study was carried out in one of the fragments (16.24 ha) close to a camping area. Initially, we searched for *Loxosceles* in all of the trees (native and exotic) present in the fragment but spiders were present only in five of 20 *Eucalyptus* trees planted at the border of the forest fragment. The vegetation around the *Eucalyptus* was essentially grass and small herbaceous plants.

Webs containing the remains of prey present in holes, hollows and bark peels from five *Eucalyptus* (up to 7 m above ground level) and the fauna present in the same places, were sampled. *Loxosceles intermedia* webs consist of a central area with a larger concentration of silk from which radiate irregular sticky threads of varying thickness. The webs cover the surface where the spiders live. The

form and size of the webs depend on the substratum on which the web is built.

Abandoned webs with remains of food were collected and prey items were removed with forceps from webs with the spider present. We did not distinguish webs of adults and juveniles, nor if the spider present in the web was the same in successive samples. We considered as associated fauna the animals present in the same microhabitat as *L. intermedia* webs; these animals were collected through visual search and with the use of forceps and fixed in 70% alcohol. The identity of animals that we could not collect was recorded. The material is deposited in the Arachnological collection of Dra. Vera Regina von Eicksted in the section of poisonous arthropods of the Imunologic Production and Research Center (SESA-PR), Piraquara, Paraná, Brazil.

In the urban building, visits were undertaken every 15 days to the garage of a masonry house located within the urban perimeter of Curitiba (25°23'28.3"S, 49°17'28.2"W). The spiders were present in a pile of lumber of 100 cm height, 200 cm width and 40 cm depth, placed against a wall. The method of collection of the prey and of the associated fauna was the same as that used in the trees.

During the study period we sampled 91 webs in the forest and 40 in the garage. The webs of *Loxosceles* species capture a wide range of invertebrate prey, with the range of potential prey groups in the forest being greater than in the building. Of the 55 prey groups sampled, 27 (49%) were exclusive to the forest, 3 (5.4%) were exclusive to the building, and 25 (45%) occurred in both habitats (Table 1). The greater prey richness in the forest ($\chi^2_{(1)}$ = 6.2, $P < 0.01$) reflected the larger variety of microhabitats, and the greater diversity, abundance and proximity of vegetation, although the Sorensen similarity index of the prey captured in the building and in the forest was rather high (0.64). Thus, spiders that colonized the building did not have access to the same prey richness, but more than 50% of the prey was similar to the prey in the forest.

The 693 prey items found in *L. intermedia* webs represented five invertebrate groups, Insecta being the dominant group in both habitats (Table 1). Levi & Spielmann (1964) reported that virtually all Arthropoda that occurred in a basement site were represented in the webs of *L. laeta*. Likewise, for *L. intermedia*, only nine higher taxa in the forest and one in the building were not recorded in the webs (Table 1). This demonstrates a low selectivity of the *L. intermedia* web.

The diet of *L. intermedia* often contains taxa rejected by other spiders. For *L. intermedia*, we recorded the capture of groups considered to be antagonist enemies of spiders, including wasps (Pompilidae and Ichneumonidae) and ants (Formi-

cidae), as well as chemically noxious taxa such as Chrysomelidae, Pentatomidae, Opiliones, Heteroptera and Staphylinidae. The capture of heavily sclerotized or dangerous prey has been recorded for other species of *Loxosceles* (*L. laeta*: Levi & Spielmann 1964; *L. reclusa*: Hite et al. 1966). According to Riechert & Harp (1987), the degree to which potentially injurious or large prey are taken varies with local prey abundance and the relative availability of different prey types. In the present study, Corinnidae, Salticidae and Opiliones were captured in a period of low resource availability, i.e. at a time when no other prey were found in the webs.

Cannibalism was recorded once in the forest for a female spider that ate a juvenile. We also found a dead female without an abdomen in an *L. intermedia* web. This spider appeared to have been eaten by a conspecific. No cannibalism or dead spiders occurred in *L. intermedia* webs in the building.

Of the 36 invertebrate groups (n = 1427 animals) collected alive near the webs of *L. intermedia*, 22 were exclusive to the forest, 14 were present in both habitats, and none was exclusive to the building. Pholcidae, Salticidae, Selenopidae and Theridiidae were the most frequent Araneae families. Even so, only Corinnidae and Salticidae occurred as prey in the webs. When the amount of food was high (identified by the presence of many prey in the webs), *L. intermedia* shared the microhabitat with other Arachnida but did not use them as prey. The spiders Selenopidae and Eusparassidae, although frequent in the trees, were not found in *L. intermedia* webs (Table 1). The fauna associated with the wood dumps in the garage was less diversified than that in the trees. Of the invertebrate groups recorded alive, only lepidopteran larvae were not found in the webs. As in the forest, the Araneae families Salticidae, Pholcidae and Araneidae were abundant (Table 1).

In the forest, two vertebrates were confirmed as predators of *L. intermedia*: *Sinax* gr. *rubra* (Amphibia, Hylidae) and the bat *Eptesicus brasiliensis* (Mammalia, Vespertilionidae). The identification was based on analysis of fecal pellets, which contained fragments of exoskeleton. The presence of amphibians (Leptodactylinae), lizards (Squamata) and six nests of a bird (insect predator) found in the hollows of *Eucalyptus*, suggested that these could also be potential predators (Table 1). Foelix (1996) considered amphibians and reptiles to be important spider predators. Delgado (1966) recorded the gecko *Tapidurus peruvianus* as a predator of *L. rufipes* in Peru. There are few mammalian predators of spiders, e.g., shrews and bats, although the South American woolly monkey *Lagothrix* apparently prey on a poisonous *Loxosceles* with no adverse effects (Foelix 1996). Two *L. intermedia* were observed being eaten by ants (subfamily Myrmicinae).

Table 1.—Number of prey items collected in *L. intermedia* webs and the associated fauna (AF, fauna collected in the same microhabitat as *L. intermedia* webs) in urban forest and in a building. Numbers indicated at order level are the sums of catches given at family level.

Taxon	Forest		Building	
	Prey	AF	Prey	AF
PLATYHELMINTHES				
Turbelaria	—	6	—	—
ANNELIDA				
Oligochaeta	1	—	—	—
MOLLUSCA				
Gastropoda	—	2	—	—
CRUSTACEA				
Isopoda	84	315	40	60
INSECTA				
Thysanura	—	3	—	—
Collembola	1	—	—	—
Blattariae	7	3	10	2
Isoptera	3	—	1	—
Orthoptera	—	2	5	4
Gryllidae	—	2	5	4
Hemiptera	7	11	2	0
Aradidae	2	—	—	—
Corimelaenidae	—	—	—	—
Cydnidae	—	—	1	—
Miridae	1	—	—	—
Pentatomidae	1	1	—	—
Reduviidae	2	10	—	—
Scutelleridae	1	—	—	—
Nymph	—	—	1	—
Homoptera	1	5	—	—
Cicadidae	1	5	—	—
Psocoptera	—	4	—	—
Coleoptera	51	8	28	1
Carabidae	—	2	2	—
Cerambycidae	4	—	1	—
Chrysomelidae	12	1	3	—
Curculionidae	1	—	1	—
Elateridae	3	—	5	1
Lampyridae	—	—	1	—
Passalidae	3	—		
Scarabaeidae	1	3	1	—
Scolytidae	3	—	1	—
Staphylinidae	3	—	2	—
Tenebrionidae	1	02	—	—
Various Fragments	20	—	11	—
Hymenoptera	145	117	77	52
Apidae (Meliponinae)	6	—	1	—
Braconidae	13	—	2	—
Formicidae	93	97	69	52
Ichneumonidae	1	—	—	—
Monomachidae	16	—	—	—
Pompilidae	3	—	—	—
Vespidae	1	20	—	—

Table 1.—Continued.

Taxon	Forest		Building	
	Prey	AF	Prey	AF
Various Fragments	12	—	5	—
Diptera	39	0	11	0
Acalyptradae	1	—	2	—
Anosopodidae	1	—	1	—
Asilidae	1	—	—	—
Bibionidae	7	—	—	—
Culicidae	1	—	1	—
Muscidae	3	—	2	—
Mycetophilidae	1	—	—	—
Phoridae	3	—	—	—
Phsychodidae	3	—	—	—
Sciaridae	3	—	—	—
Stratiomydae	12	—	1	—
Tabanidae	1	—	—	—
Tipulidae	2	—	2	—
Various Fragments	—	—	2	—
MYRIAPODA				
Diplopoda	1	—	—	—
Chilopoda	—	4	—	—
ARACHNIDA				
Opiliones	6	184	—	—
Pseudoescorpiones	1	24	—	—
Araneae	4	438	0	81
Araneidae	—	49	—	6
Ctenidae	—	14	—	—
Lycosidae	—	10	—	1
Pholcidae	—	46	—	27
Theridiidae	—	67	—	—
Corinidae	2	3	—	—
Eusparassidae	—	7	—	—
Salticidae	1	156	—	47
Selenopidae	—	86	—	—
Thomisidae	—	1	—	—
CHORDATA				
Amphibia	2	6	—	—
Leptodactylidae	—	2	—	—
Hylidae	—	4	—	—
Reptilia	—	1	—	—
Mammalia	—	4	—	—
Vespertionidae	—	4	—	—

However, it was not possible to determine whether the ants had killed these spiders or if the spiders had died from other causes. We have not detected any potential predators (occasional or common) of *L. intermedia* in residential areas of Curitiba.

The results of this study indicate that *L. intermedia* is a generalist feeder that uses a low-cost sit-and-wait predation strategy. The urban habitat provides more than 50% of the prey types found in the natural habitat, it has a lower density of other spiders (Table 1) and a possible lack of natural ene-

mies. All these factors probably contribute to the persistence of *L. intermedia* in urban areas.

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SHORT COMMUNICATION

PLATOCOELOTES POLYPTYCHUS, A NEW SPECIES OF HACKLED MESH SPIDER FROM A CAVE IN CHINA (ARANEAE, AMAUROBIIDAE)

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ABSTRACT.   A new species of hackled mesh spider, *Platocoelotes polyptychus* (Araneae, Amaurobiidae), is described and illustrated based on specimens from Gufengdong Cave, Hunan Province, China.

Keywords: Taxonomy, Oriental region, morphology, caves

During our exploration of the Gufengdong Cave, Liuyang County, Hunan Province, China in 2003 and 2004, we encountered several specimens of a coelotine spider living within the cave. The presence of a posterior apophysis extending from the conductor and the absence of a median apophysis suggests that this new species may be a member of the genus *Platocoelotes* Wang 2002, but the lack of two patellar apophyses, the presence of a short cymbial furrow, and the very different female genitalia suggests that this placement may be incorrect. In fact, this new species is also similar to the members of *Spiricoelotes* Wang 2002 in having a long, linear embolus, a strongly curved patellar apophysis and in having no epigynal teeth, but the presence of the atrial septum, the indistinct spermathecal stalks and bases, the short cymbial furrow, the bifurcated conductor with several apophyses, prevent it from being placed in *Spiricoelotes*. We present here a description of the new species, which we tentatively place in this genus, despite the differences cited above.

Abbreviations used in the text: ALE = anterior lateral eye; AME = anterior median eye; AW = anterior width (of the MOQ); MOQ = median ocular quadrangle; PLE = posterior lateral eye; PME = posterior median eye; PW = posterior width (of the MOQ); RTA = retrolateral tibial apophysis. All measurements are given in millimeters. Eye diameters are taken at the widest point. Leg measurements are shown as: total length (femur, patella, tibia, metatarsus, tarsus). The terms used in the text and figure legends mainly follow Wang (2002). All the type specimens are deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS).

Family Amaurobiidae Thorell 1870
Platocoelotes Wang 2002

Type species.—*Coelotes impletus* Peng & Wang, 1997, by original designation.

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Remarks.—The genus *Platocoelotes* was erected and revised by Wang (2002, 2003) and includes five species: *P. impletus* (Peng & Wang 1997), *P. icohamatoides* (Peng & Wang 1997), *P. icohamatus* (Zhu & Wang 1991), *P. kailiensis* Wang 2003, and *P. lichuanensis* (Chen & Zhao 1998). The genus is currently confined to China.

Platocoelotes polyptychus new species
Figs. 1–10

Material examined.—CHINA: *Hunan Province*: Holotype male, Gufengdong Cave, Gaoping Town, Liuyang County (28.1° N, 113.6° E), China, 31 February 2004, Xiang Xu (IZCAS). Paratypes: 1 female and 5 males, same locality as holotype; 1 female, same locality as holotype, 8 October 2003, Shuqiang Li, Guo Tang and Yufa Luo (IZCAS).

Figure 1.—*Platocoelotes polyptychus* new species: a juvenile spider on a stalactite within Gufengdong Cave.

Figures 2–10.—*Platocoelotes polyptychus* new species. 2. Male, eye, anterior view; 3. Male, chelicera, ventral view; 4. Male palp, prolateral view; 5. Male palp, ventral view; 6. Male palp, retrolateral view; 7. Male, conductor, retrolateral view; 8. Male, conductor, prolateral view; 9. Female, epigynum; 10. Female, vulva. Scale lines: 0.5 mm (Figs 2–6, 9, 10); 0.1 mm (Figs 7, 8). Abbreviations: AS = atrial slit; ASE = atrial septum; C = conductor; CD = copulatory duct; CDA = conductor dorsal apophysis; CF = cymbial furrow; E = embolus; FD = fertilization duct; H = hood; PA = patellar apophysis; RTA = retrolateral tibial apophysis; S = spermathecae; SH = spermathecal head; ST = subtegulum; T = tegulum; TS = tegular sclerite.

Etymology.—The species name refers to the crinkly surface of the conductor.

Diagnosis.—Males can be distinguished from other *Platocoelotes* by the presence of only one patellar apophysis, the short cymbial furrow, and the long, slender, strongly bifurcated conductor. The female is diagnosed by the short epigynum, the anteriorly situated epigynal hoods, and the very different vulva (Figs. 9–10).

Description.—*Male (holotype):* Total length 8.50. Carapace 4.40 long, 3.00 wide; abdomen 4.10 long, 2.20 wide. Carapace light yellow. Eye measurements (Fig. 2): AME 0.13; ALE 0.18; PME 0.15; PLE 0.15; AME–AME 0.05; AME–ALE 0.08; PME–PME 0.13; PME–PLE 0.15; MOQL 0.38, AW 0.35, PW 0.43; Clypeus 0.20. Chelicerae with 2 promarginal teeth and 5 retromarginal teeth (Fig 3). Leg measurements: I 17.00 (4.30 + 1.40 + 4.30 + 4.30 + 2.70); II 15.40 (3.90 + 1.40 + 3.60 + 4.00 + 2.50); III 15.15 (3.90 + 1.30 + 3.35 + 4.25 + 2.35); IV 20.05 (5.05 + 1.45 + 4.65 + 6.00 + 2.90). Male palp with sharply curved patellar apophysis; RTA with distal end extended beyond tibia; lateral tibial apophysis absent; cymbial furrow short, conductor distinctly bifurcated, with numerous shallow grooves on the surface and posteriorly extended wing-like apophysis; conductor dorsal apophysis flat; embolus posterior in origin, long, linear; median apophysis absent (Figs 4–8).

Female (paratype): Total length 8.50. Carapace 4.40 long, 2.90 wide; abdomen 4.10 long, 2.60 wide. AME 0.13; ALE 0.18; PME 0.15; PLE 0.15; AME–AME 0.08; AME–ALE 0.10; PME–PME 0.15; PME–PLE 0.15; MOQL 0.35, AW 0.33, PW 0.45; Clypeus 0.30. Chelicerae with 3 prolateral teeth and 5 retrolateral teeth. Leg measurements: I 15.80 (4.20 + 1.50 + 3.80 + 3.80 + 2.50); II 14.80 (4.00 + 1.40 + 3.40 +3.70 + 2.30); III 13.70 (3.60 + 1.30 + 3.00 + 3.80 + 2.00); IV 18.30 (4.70 + 1.40 + 4.30 + 5.30 + 2.60). Epigynum without epigynal teeth; atrium with atrial septum; hoods situated anteriorly; spermathecae strongly convoluted, with indistinct stalks and bases; spermathecal heads thumb-shaped, situated laterally; copulatory ducts long, looped (Fig 9–10).

Distribution.—Known only from the type locality, a cave situated in Hunan Province. Based on the light body color, *Platocoelotes polyptychus* is considered to be troglobitic, but further study will be necessary.

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SHORT COMMUNICATION

SEASONAL VARIATION IN PARASITISM BY *LEPTUS* MITES (ACARI, ERYTHRAEIDAE) UPON THE HARVESTMAN, *LEIOBUNUM FORMOSUM* (OPILIONES, SCLEROSOMATIDAE)

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ABSTRACT. We recorded the number of ectoparasitic erythraeid mite larvae (*Leptus* sp. Latreille 1796) that were attached to 1241 *Leiobunum formosum* Wood 1870 from a population in southeastern Virginia. The prevalence of infestation (percent of individuals parasitized) exhibited significant annual and seasonal variation, ranging from 0.5% to 20.3%. The mean intensity of infestation (number of mites per parasitized individual) varied from 1.0 to 1.3, with a maximum observed intensity of 3 mites/individual. This study provides the first description of annual and seasonal variation in mite infestation of harvestmen.

Keywords: Harvestmen, ectoparasites, mites, eryrthraeids, variation

The larvae of erythraeid mites of the genus *Leptus* are common ectoparasites of a variety of arthropods, including harvestmen (Southcott 1992; Cokendolpher 1993; Mitov 2000). Although these mites are assumed to feed upon hemolymph (Åbro 1988), researchers know little about the impact of mites upon the survival, locomotion, or reproductive capacity of their opilionid hosts (Guffey 1998). Prior studies of the interactions of erythraeid mites and harvestmen have focused on the mode of attachment by mites (Åbro 1988), preferences of mites for specific attachment sites (McAloon & Durden 2000; Mitov 2000), and the ecological significance of variation in mite infestation rates between syntopic species (Guffey 1998). Reported values for the prevalence of mite parasitism (fraction of individuals infested) vary from 11% for *Leiobunum vittatum* in Louisiana (Guffey 1998) to 61% for *L. formosum* in Tennessee (McAloon & Durden 2000). Similarly, the intensity of mite infestation (mean number of mites per infested individual) ranges from 2.3 for *L. formosum* (McAloon & Durden 2000) to nearly 4 for *L. nigripes* (Guffey 1998). Reported maximal intensities of infestation have ranged from 14 mites for *L. formosum* (McAloon & Durden 2000) to 32 mites for *Zachaeus crista* (Mitov 2000).

Relatively few studies have examined seasonal variation in parasitism upon harvestmen. In Japan, infestation by gregarines has been observed to vary between seasons for *Leiobunum manubriatum* and between populations for *L. manubriatum* and *L. globosum* (Tsurusaki 1986). In an effort to assess seasonal variation in the prevalence and intensity of

larval mite infestations amongst harvestmen, we studied a population of *L. formosum* Wood (1868), which occurs on the campus of Virginia Wesleyan College (VWC) over a period of 14 months (9 October 2003–11 November 2004). In southeastern Virginia, *L. formosum* is one of the most commonly encountered species of harvestman and inhabits pine and mixed mesic hardwood forests (personal observation). This species occurs throughout the southeastern U.S.A., and has a geographic range that extends from Florida north to Ontario and west to Colorado (Cokendolpher & Lee 1993). In contrast to other eastern species of harvestmen, *L. formosum* exhibits an atypical life history in which adults do not perish in the autumn (following mating) but instead overwinter (Comstock 1948). Thus, late spring and early summer populations frequently consist of both juveniles and adults.

Leiobunum formosum is an ideal species for a comparative study of mite parasitism because data regarding the prevalence and intensity of mite infestation for a Tennessee population of this species has already been published (McAloon & Durden 2000). In addition, Cokendolpher (1993) noted a record of infection for *L. formosum* by the mite, *Leptus indianensis*, in nearby Wakefield, VA (approximately 76 km west of our study site). The southeastern Virginia population of *L. formosum* that we examined in this study, thus, may be infested by the larvae of the same species of *Leptus* as the Tennessee population of McAloon & Durden (2000).

In 2003, we captured and released 241 adult *L. formosum* 9 October–22 November. Each individual

Table 1.—Frequency distribution of *L. formosum* hosts with different numbers of larval erythraeid mites attached.

Number of Mites Present	Number of *L. formosum* Autumn 2003	Number of *L. formosum* Summer 2004	Number of *L. formosum* Autumn 2004
0	192	656	393
1	39	3	10
2	6	0	0
3	4	0	0

was carefully examined and the number of larval mites on each harvestman was recorded. In 2004, we collected 291 juvenile and 368 adults from the trunks of pine trees (*Pinus taeda*) and hardwoods, including hickory (*Carya* sp.), red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), white oak (*Quercus alba*), and dogwood (*Cornus florida*). These individuals were preserved in 70% ethanol immediately following capture. In January 2005, each of these harvestmen was carefully examined with a stereomicroscope and the number of mites infecting each individual was recorded (this procedure follows that of McAloon & Durden 2000). In addition, from 21 September–11 November 2004, we captured, sexed, and released 290 adults. We also captured and preserved an additional 103 adults from the trunks of nearby pine and hardwood trees from 5 October–4 November 2004. The prevalence and intensity of mite infection for these individuals was determined in February 2005.

The results of our study (Table 1) indicated that the prevalence of larval mite infestation varied dramatically between our three sampling periods ($\chi^2 = 160.0$, $df = 2$, $P < 0.001$). Mite infestation was significantly more prevalent for Autumn 2003 than for either Summer ($\chi^2 = 128.1$, $df = 1$, $P < 0.001$) or Autumn 2004 ($\chi^2 = 59.5$, $df = 1$, $P < 0.001$). Our results also indicated that mite infestation was significantly more prevalent in Autumn than in Summer 2004 ($\chi^2 = 8.2$, $df = 1$, $P = 0.004$). In Autumn 2003, the VWC campus population of *L. formosum* exhibited an infestation rate of 20.3%. In contrast, the overall parasitism rates for Summer and Autumn 2004 were only 0.5% and 2.5%, respectively. The intensity of infestation (mean number of mites per parasitized individual) also varied between samples (Table 1). In 2003, the intensity was 1.3, with four observations of hosts infested with 3 mites (the most intense infestations that were observed). During 2004, the intensity for both summer and autumn samples was only 1.0 (no individual was found with more than 1 mite). Unfortunately, we do not have data with regards to the sex of the harvestmen for 2003, but for Summer 2004 only 2 females (out of 173) had a mite and no males (out of 195) were infected. For Autumn 2004, there

was no difference in the prevalence of mites between males (243: 0 mites, 5: 1 mite) and females (150: 0 mites, 5: 1 mite). In addition, there was no measurable difference in mite infestation between adults (2 females had 1 mite) and juveniles (1 individual had 1 mite) for the summer sample.

In comparison to the studies of Guffey (1998) and McAloon & Durden (2000), our investigation revealed a considerably lower prevalence and intensity of mite infestation. The ecological significance of this variation is difficult to assess because no adverse effects of ectoparasitic mites upon harvestmen physiology or reproductive success have yet been empirically demonstrated (Guffey 1998). For dipterans, Polak & Markow (1995) found that ectoparasitic mites can severely impair the reproductive activities of individual flies, particularly males, and thus, high intensity mite infections can have serious consequences for individual fitness. However, other studies of ectoparasitic mites have revealed no measurable adverse effects upon the reproduction or survival of host species (Pacejka et al. 1998; Reardon & Norbury 2004). Therefore, further research on the physiological consequences of mite infestation upon harvestmen is required.

Our findings of variation (in comparison to the population of *L. formosum* examined by McAloon & Durden 2000) in the prevalence and intensity of mite infestation may reflect differences in local population densities of either harvestmen or parasitic mites. Similarly, variation in habitat use and activity patterns (Edgar & Yuan 1968; Edgar 1971) could produce differences in the risk of exposure to larval erythraeid mites and consequently generate intra- and interspecific variation in the prevalence or intensity of infestation. Most adult harvestmen at our study site were collected from above ground habitats. Occupation of these areas may minimize contact with the leaf litter, thereby reducing contact with larval mites, and thus contributing to the overall low prevalence and intensity of mite infection that we observed.

Seasonal or annual variation in mite infestation has been observed in other hosts (Morlan 1952; Howell et al. 1957; Shah 2001; Harris et al. 2003), but its significance is not completely understood.

Dramatic seasonal changes in both temperature and humidity have been identified as major contributors to variation in the sizes of mite populations (Boyne & Hayne 1983; Shah 2001). Differences in the prevalence or intensity of mite infestation may also reflect variation in the life history of the parasite. In erythraeid mites, the larvae (but not the adults) are parasitic (Southcott 1992; Cokendolpher 1993). Hence, seasonal variation in infestation may simply reflect periods in the year when larval mites are particularly common or relatively rare. Additional field and laboratory studies of the life history and ecology of parasite and host species are required before the significance of geographical, seasonal, and annual variation can be fully understood.

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SHORT COMMUNICATION

DESCRIPTION OF THE MALE OF *PLECTREURYS ARIDA* (ARANEAE, PLECTREURIDAE)

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ABSTRACT.   The first known males of the spider *Plectreurys arida* Gertsch are described from the xeric shrub habitats and houses of Baja California Sur, México. Males have a smaller carapace and abdomen than females. The length and spination formula of the first leg differ from females; the first legs are longer, and the chelicerae have stridulating grooves in males.

Keywords: *Plectreurys*, Mexico, Baja California, taxonomy

The family Plectreuridae is recorded only from North America and Cuba where they inhabit arid zone habitats from southeastern United States and Cuba to southeastern Mexico. Plectreurids are often considered a relictual family of haplogyne spiders and are currently grouped in two genera, *Kibramoa* Chamberlin 1924 and *Plectreurys* Simon 1893. The latter genus contains 18 species from North America, nine of them known from Mexico, with four from the Baja California Peninsula: *P. tecate* Gertsch 1958, *P. valens* Chamberlin 1924, *P. bicolor* Banks 1898 and *P. arida* Gertsch 1958 (Gertsch 1958; Platnick 2004).

Originally, specimens of *P. arida* were identified by Chamberlin (1924) as *P. tristis* 1893 from Sonora, the Baja California Peninsula, and adjacent islands in the Gulf of California. Gertsch (1958), in his revision of the family Plectreuridae, assumed that these species and some specimens determined as *P. valens* by Chamberlin (1924) and assigned them to *P. arida* as a new species, with a distribution restricted to the state of Baja California Sur and some islands in the Gulf of California. In this same work, several species of *Plectreurys*, including *P. arida*, were added to the tristis group, as the male palps exhibit a spherical bulb with a long, thin and, in some specimens, coiled embolus, and a coupling spur is present on the first tibia of the males. Concerning the biology of *P. arida*, it is known that this species has been collected under stones in localities near the shore line and also in canyons, without specifying its microhabitat.

Only females of *P. arida* have been described from the Baja California Peninsula. Here, the first description of males is presented. Females and males were collected by hand and with pitfall traps

in xeric shrubs near two oases and houses in Baja California Sur.

Measurements (in mm) were taken using a standard ocular grid with a Zeiss dissecting stereomicroscope, following the format of Gertsch (1958). Drawings were prepared with a camera lucida. Specimens are lodged in the California Academy of Sciences, San Francisco (CAS), National Collection of Arachnids in the Instituto de Biología, Universidad Nacional Autónoma de México (CNAN), and the Arachnid Collection in the Centro de Investigaciones Biológicas del Noroeste (CACIB).

Family Plectreuridae Simon 1893
Genus *Plectreurys* Simon 1893
Plectreurys arida Gertsch 1958
Figs. 1–4

Plectreurys arida Gertsch 1958: 26–27, fig. 90.

Type specimen.—Holotype female, Ballena Island, *Baja California Sur*, MEXICO, 24°29′N, 110°25′W, 9 June 1921, J.C. Chamberlin (CAS, not examined).

Material examined.—MEXICO: *Baja California Sur*: 2 ♂, 2 ♀, La Purísima, 112°02′54″N, 6°12′23″W, elevation 291 m, 16 June 2003, M. Correa (CACIB; 1 ♂ in CNAN); 2 ♀, Cd. Constitución, 111°40′15″N, 25°01′57″W, 21 April 1996, R. Domínquez (CACIB).

Diagnosis.—*Plectreurys arida* resembles *P. bicolor* in body structure and in the spherical bulb of palp with coiled embolus. It differs from *P. bicolor* in having a shorter, stouter, and distally more curved embolus, and from *P. valens* in having an epigynum that is wider than long. The males are assigned to *P. arida* because both sexes were collected together and the females were used to con-
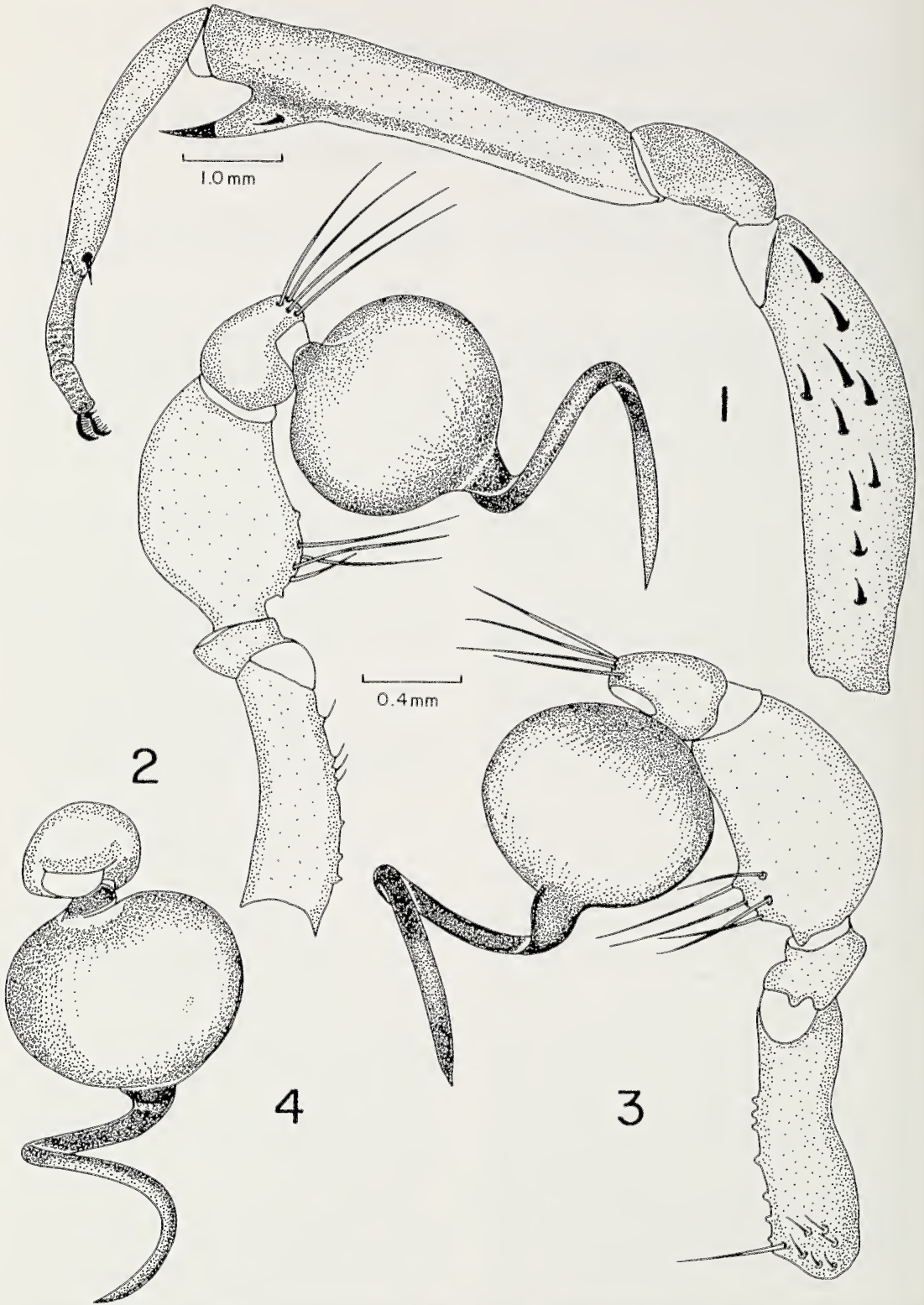
Figures 1–4.—*Plectreurys arida* Gertsch. 1. First right leg of male, prolateral view; 2. Right palp, retrolateral view; 3. Right palp, prolateral view; 4. Bulb, frontal view.

firm the identification against the original description by Gertsch (1958).

Description.—*Males (n = 2):* Total length 7.8–8.4 mm, carapace, chelicerae and legs shiny mahogany brown. Carapace almost smooth with few uncolored hairs. Carapace length 3.8–4.1 mm, 2.5–2.9 mm wide. Anterior eye row weakly procurved from frontal view and almost straight; median eyes separated by their radius and almost two diameters from lateral eyes, which are larger by ratio of 6.6. Posterior eye row slightly recurved, oval median eyes separated by their diameter, as well as from lateral eyes. Ocular quadrangle broader than long narrower in front. Clypeus curved sloping in front, with a height of five diameters of anterior median eye. Chelicerae with stridulating grooves in retrolateral view. Sternum 2.0–2.4 mm long 1.5–1.7 mm wide. First pair of legs longer stouter than others. Femur I, 4.5–4.8 mm; patella I, 1.5–1.7 mm; tibia I, 4.3–48 mm; metatarsus I, 2.5–3.0 mm; tarsus I, 1.3–1.5 mm. Tibia and patella IV, 5.8–6.5 mm. Ratios of width to length of segments of first leg: femur, I 4/2; patella, 1/ 2.0; tibia 1/5; metatarsus 1/ 10.4. Spines of first leg: femur with 10 prolateral; tibia with prolateral spine near base and strong retrolateral spur ending in stout spine; metatarsus with short robust prolateral spine. First metatarsus and tarsus curved, latter with false sutures in distal half. Tibia II with 2-2-2-2 spines and metatarsus II with 1-1-1-2; paired claws of first tarsus with 8 teeth; unpaired with one denticle. Abdomen 4.0–4.3 mm long 3.0–3.4 mm wide, gray in color, with black, thin setae; epigastrium more sclerotized than in females. Palps with spherical bulb with tubular long thin embolus which forms basal coil then curves distally, length of embolus not exceeding length of bulb.

Distribution.—This species is known only from Baja California Sur and adjacent islands in the Gulf of California.

Natural history.—Males, female and juveniles were captured by hand and with pitfall traps during April, June, and November in xeric shrub land areas and in houses. One female was captured under stones in a tubular burrow 30 cm deep, and the entrance was covered with silk; one male was collected while wandering at night and four juveniles collected from pitfall traps. During an annual sampling (2002–2003), only eight specimens were collected, probably because the population is very small or sedentary, remaining in their burrows to avoid the high temperatures of this area.

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